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CONTENTS

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ASPECTION IN THE BIOTIC COMMUNITIES OF THE CHURCHILL AREA, MANITOBA

H. ELLIOTT McCLURE
Ord, Nebraska

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ASPECTION IN THE BIOTIC COMMUNITIES OF THE CHURCHILL AREA, MANITOBA

INTRODUCTION

During the summer of 1936 a study of the invertebrate population of the tundra and "bush" was undertaken at Churchill, Manitoba, from June 7 until August 4.

Churchill is situated on a narrow peninsula between the mouth of the Churchill River and Hudson Bay. The mouth of the river, which flows due north at this point, is a little over a half mile wide, but seven miles south of the mouth, the river opens into Churchill Bay, which is at some points three miles across. Churchill is at 59° north latitude, and these two bodies of very cold water maintain the temperature of the air at such low levels that only tundra plants can live in this area.

Three miles south of Churchill the terrain is covered with open stunted black spruce-tamarack forest which is interspersed with patches of tundra. The soil is gravel or precambrian granite overlaid with a layer of varying thickness of sphagnum which is frozen the year around, although during the summer it thaws to a depth of several inches. The shore of Hudson Bay alternates with outcroppings of granite and gravel beach. Figure 1 shows the position of the town in relation to these granite hills. Because of the abundance of snow and ice during nine months of the year, the tundra is so heavily dotted with lakes and ponds that it is impossible to walk in a straight line for any distance. The length of time in the summer during which temporary pools remain varies from year to year, for in 1936 they were present during the entire period of observation, while in 1937 they had dried up considerably by the middle of August.

The Churchill River carries very little silt, and at this point has a hard bed. The mouth and bay are deep, and, since Hudson Bay is navigable for at least a month, large ocean-going freight boats may enter the fresh-water bay. The Canadian Government has built a large grain elevator at Churchill. During several months of the year grain from Saskatchewan is shipped here for future passage to Europe. Hence, during the summer Churchill (Fig. 2) has a population of three or four hundred people, but during the winter from thirty to fifty. Most of the permanent residents are traders and hunters.

In view of the extensiveness of the collections at Churchill and the desirability of accuracy in the determination of species, the writer made no attempt to name any species. After returning to the United States, correspondence with 63 specialists was undertaken and the collections of the respective groups in which they were interested were sent to them. I wish to express my sincere appreciation of the splendid cooperation which I received from these men. It was only through their kind offerings of time and knowledge that this paper was made possible.

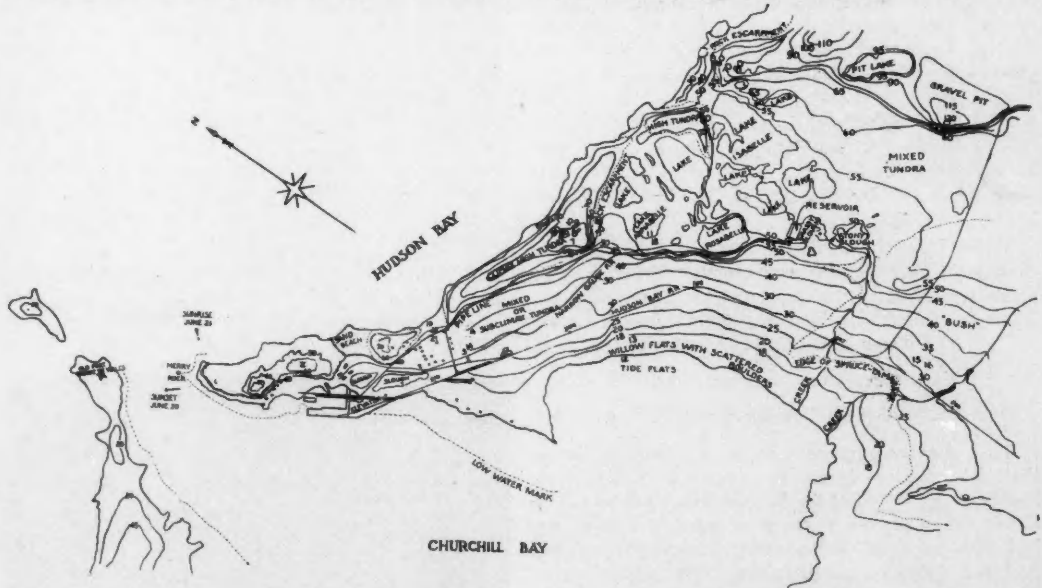

FIG. 1. Map of the region of Churchill, Manitoba. Scale shown by mile numbers on railway, Churchill being mile 510.

Determinations were made by the following systematists: Dr. C. P. Alexander, Tipulidae; Dr. A. W. Baker, Mallophaga; Dr. F. C. Baker, Mollusca; Dr. A. W. Bell, Aquatic Annelida; Dr. H. C. Bold, Algae; Dr. A. G. Boving, Coleoptera larvae; Dr. E. P. Breaky, Fulgoridae and Cicadellidae; Dr. W. J. Brown, Coleoptera; Mrs. Beirne B. Brues, grasses; Dr. J. S. Caldwell, Chermidae; Dr. J. C. Chamberlin, pseudoscorpions; Dr. R. V. Chamberlin, Araneida; Dr. R. E. Coker, Copepoda; Dr. A. C. Cole, Jr., Formicidae; Dr. R. A. Cushman, Ichneumonoidea; Dr. H. E. Ewing, Hydracarina; Dr. E. P. Felt, Cedidomyidae; Dr. M. S. Ferguson, Anostraca; Dr. C. L. Fluke, Syrphidae; Mr. A. C. Frederick, Lepidoptera; Dr. Theo. H. Frison, Bombidae; Dr. Harry J. Fuller, plants; Dr. A. B. Gahan, Chalcidoidea; Dr. Philip Garman, Acarina; Dr. G. J. Goodman, flowering plants; Dr. H. M. Harris, Nabidae; Dr. L. Haseman, Psychodidae; Dr. Morgan Hebard, Orthoptera; Dr. Carl Heinrich, Lepidoptera adults and larvae; Dr. E. M. Heiss, Syrphidae; Dr. C. C. Hoff, Ostracods; Dr. Leslie Hubricht, Amphipoda; Dr. H. B. Hungerford, Corixidae; Dr. Libbie L. Hyman, Turbellaria; Dr. F. P. Ide, Ephemerida; Dr. Chancey Juday, Cladocera; Dr. H. H. Knight, Hemiptera; Dr. E. F. Knipling, Diptera larvae; Dr. S. F. Light, Copepoda; Dr. Ruth Marshall, Hydracarina; Dr. Robert Matheson, Culicidae; Dr. M. C. Meyer, Hirudinea; Dr. Harlow B. Mills, Collembola; Dr. B. Elwood Montgomery, Odonata; Dr. C. F. W. Muesebeck, Braconidae; Dr. P. W. Oman, Cicadellidae and Fulgoridae; Dr. H. A. Rehder, Mollusca; Dr. Carl P. Schmidt, Anura; Dr. John C. Schread, Hymenoptera; Dr. H. H. Schwardt, Tabanidae; Dr. Frank Shaw, Mycetophilidae; Dr. John B. Steinweden, Thysanoptera; Dr. J. A. Stevenson, Fungi; Dr. M. A. Stewart, Siphonaptera; Mr. L. G. Strom, Aphididae; Mr. C. R. Twinn, Simuliidae.

In addition to those in the foregoing list, the following have died since they cooperated with me in this work: Dr. H. C. Fall, Coleoptera; Dr. Ralph Voris, Staphylinidae; Dr. W. M. Wheeler, Formicidae; Dr. A. P. Jacot, Acarina; Dr. Grace A. Sandhouse, Sphecidae.

Major J. G. MacLachlan kindly allowed us the use of Hudson Bay Railway equipment, and Mr. George Couts furnished us with maps of the Churchill area. Dr. V. E. Shelford helped in the organization of the writer's expedition and read the first draft of this paper.

EQUIPMENT AND METHODS

The writer accompanied Dr. A. C. Twomey, ornithologist, and we were given access to a furnished house-car by the Hudson Bay Railway officials. As it was not necessary to conserve space or weight, we had with us about 200 pounds of equipment. This included clothing, collecting equipment, utensils, etc. Food was, of course, available at the stores and trading posts. A complete list of the equipment taken has already been published (McClure 1937).

Upon arriving at Churchill on June 9, the tundra was immediately examined and collecting stations at 21 different habitats were set up (Fig. 1). Once each week each of these stations was visited. These were distributed over an area of several square miles, and it was not possible to visit them all each day. At each terrestrial station the plants were swept with 50 sweeps of a 12-inch sweep net in order to determine the relative abundance of insects. Separate collections were made for identification purposes. At Stations 2, 3, 5, and 7, which were comparatively dry, samples of the sphagnum were collected and its occupants driven out by means of a modified Berlesi funnel (McClure 1935). At each aquatic habitat representative animals were collected and estimates made of the relative abundance. A Needham aquatic net was used.

Observations were made in the mornings, and each afternoon was spent in pinning and mounting the specimens. Altogether some 50,000 specimens were taken. At Station 3, which was in open mixed tundra, a weather station, consisting of a hygrograph and a thermograph, was set up and checked each week with a sling psycrometer. Also at Station 3 were erected a light trap and a bait trap. Various baits were used but proved ineffective, apparently because of the high winds. The light trap was also ineffective because of lack of darkness.

WEATHER

Churchill is one of the coldest spots in northern Canada, but does not have a heavy snowfall. Because of high winds, snow drifts badly, and buildings are often completely buried. In midwinter a wind of 40 miles an hour with a temperature of −70° F. (−56.6° C.) was reported as not uncommon. In 1936 the ice in Churchill Bay and on the river broke up on June 20, but in 1937 it broke on May 27, which was an exceedingly early record. It is more common for the ice to go out during the last part of June. Thawing on land was a little more rapid, therefore temporary pools were evident, but ice was still rising from the bottoms of the fresh-water lakes on June 10.

During 55 days in which observations were made, the average air temperature was 11.6° C. Humidity was exceedingly high, hence a hygrograph had to be constantly checked. The relative humidity would

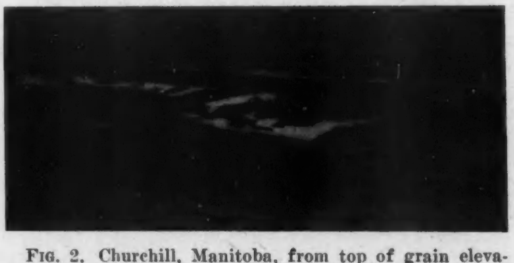

FIG. 2. Churchill, Manitoba, from top of grain elevator looking north over the postoffice on hill.

range in a single day from saturation at night to 35 percent or less at midday. Probably the desiccating effect of this rapid drop in relative humidity had little action upon the invertebrates since they could retire to the ground and to low plants. Range in temperature was far more important. The sunny side of a rock, at the base of which were many plants, would have a temperature during clear days of nearly 40° C. On clear, warm days the tundra steamed, and heat waves vibrated across it. In 1936, it will be remembered, temperatures within the United States reached an all-time high, and similarly it became quite warm at Churchill. Five days, from July 5 to 10, had an average maximum temperature of 23° C. Table 1 gives the average relative humidity and the average temperatures during the period of observation. Of the 55 days, 40 percent of the weather was clear, 20 percent partly cloudy, and 38 percent cloudy. There was rain 17 percent of the time. Only four days were calm. Table 2 presents further data concerning the weather from June 10 to August 2.

TABLE 1. Weather conditions at Churchill, Manitoba; June 10-August 2, 1936.

Date	5-Day Average Relative Humidity, Percent			Date	5-Day Average Temperature, Degree Centigrade		
	Max.	Min.	Ave.		Max.	Min.	Ave.
June 15.	96	59	77	June 10.	8	1.6	4
June 20.	100	54	80	June 15.	12	3	7
June 25.	99	51	79	June 20.	18	7.6	10
June 30.	93	36	69	June 25.	15	7	10
July 5.	94	55	77	June 30.	19	8.5	13
July 10.	92	62	79	July 5.	20	12	15
July 15.	93	45	70	July 10.	23	13	17
July 20.	93	52	75	July 15.	17	10	12
July 25.	92	45	71	July 20.	18	9	13
Aug. 2.	94	83	91	July 25.	20	10	14
				Aug. 2.	17	13	13
Average .	94	54	76	Average.	17°C. 62.6°F.	8.6°C. 47.5°F.	11.6°C. 53.0°F.

At the time of arrival, average temperature in lakes and pools was 1° C. Water temperature gradually increased until it reached its highest point (17° C.) during the week of July 12. From then until the end of the observations, water temperatures gradually dropped. Each type of pool had its own temperature range. A man-made pool, Station 1, (Fig. 3) surrounded by protective gravel banks, had the highest water temperature, while a natural lake, Lake Annabelle, Station 11, showed the greatest lag in temperature. Three permanent pools on the high tundra had like temperatures, while a flowing pool, Station 17, had a relatively invariable temperature. Table 3 gives further information concerning pool temperatures.

FIG. 3. Looking east over Churchill from top of grain elevator. Pool in foreground was Pool Station 1. Photograph taken on June 10, 1936. Note snowdrifts.

TABLE 2. Weather at Churchill, Manitoba; June 10-August 2, 1936.

Weather	Hours	Days	Percent
Clear	516	21.5	40.9
Partly Cloudy	264	11.0	20.9
Cloudy	480	20.0	38.0
Rain	218	9.0	17.3
WIND			
Strong S.	72	3.0	
Strong SE.	180	7.5	
Strong N.	192	8.0	
Total Strong	444	18.5	36.2
Medium SE.	276	11.5	
Medium E.	24	1.0	
Total Medium	300	12.5	24.5
Light E.	24	1.0	
Light SE.	48	2.0	
Light S.	132	5.5	
Light N.	108	4.5	
Light NW.	72	3.0	
Total Light	384	16.0	31.3
Calm	96	4.0	8.0

TABLE 3. Average water temperature at 10:00 A.M. in aquatic stations; Degree centigrade.

Week / Date	1 6/14	2 6/21	3 6/28	4 7/4	5 7/12	6 7/19	7 7/26	8 8/2
Station 1 Man-made pool	...	9	12.5	25	21	18	15	13
Station 8 High tundra pool	6.6	9	11.5	10	14	14	13	12
Station 9 High tundra pool	6.6	9	11.5	11.5	15	14	12	15
Station 10 High tundra pool	6.6	9	11.5	12	15	14	15	14.5
Station 11 Lake Annabelle	0	2	12	12	13	12	18	17
Station 14 Grass-filled pool	8	..	15	10.5	17.5	..	13	12
Station 17 Flowing pool	10	..	15.5	15.5	17.5	23	19	17
Temperature average	6.3	7.6	12.8	14.1	17	15	15	14
Hudson Bay, at shore	...	..	....	8	13	6	10	14

The greatest variability in temperature range existed in terrestrial habitats. At each station at each observation, air temperature at shoulder height, soil temperature at a depth of about three inches, and soil surface temperature were recorded. The peak of terrestrial temperatures was also during the week of July 12. During this week the average air temperature was 20° C., soil temperature at three inches 15° C., and soil surface temperature 23° C. There was a range of 8° C. between the soil temperature and the surface temperature. This variation was

FIG. 4. Eriophorum associes, Station 4. Plants in fruit.

TABLE 4. Temperatures in centigrade at terrestrial stations.

Week Date	1 6/14	2 6/21	3 6/28	4 7/5	5 7/12	6 7/19	7 7/26	8 8/2
Station 2–Dwarf willow associes								
Air	6.6	13.3	19	12	14.5	16	17	14
Soil	3	4.4	11.8	5.5	12	8	8	7
Surface	....	....	....	16	16	26	24	22
Station 3–Mixed tundra								
Air	5.5	10	19	11.5	16	14.5	14	13
Soil	8	8	11.5	6	12	9	7.5	8
Surface	....	24.4	33	10.5	16	30	16	22
Station 4–Eriophorum associes								
Air	5	15.5	17.2	12.5	15	15	14.5	13
Soil	4.4	9	10	14	12	16	9	10
Surface	....	....	....	20	16	24	22	22
Station 5–Climax high tundra								
Air	5.5	8	7.5	6	11	13	12.5	13
Soil	4	9	5	4	8	9	10	10
Surface	12.2	13.3	15	10	12	13	20	28
Station 6–Cranberry-lichen associes								
Air	6.6	8	7.5	7	11	13	8	13
Soil	5.5	10	12	12	14	14	17	19
Station 7–Climax high tundra								
Air	5.5	8	7.5	7	11	13	8	14
Soil	6.6	4.4	5.5	4	11	10	12	12
Surface	12.2	9	18	8	17	18	23	26
Station 12–Tide flats								
Air	....	....	....	26	28	24	15	18
Soil	....	....	....	14	14	11	12.5	11
Surface	....	....	....	33	33	33	27	17
Station 13–Black spruce clump								
Air outside clump	12.5	11	11.5	26	28	24	15	18
Air inside clump	11	9	11.5	24	26	24	16	16
Soil outside clump	8	9	16	14	14	11	12.5	11
Soil inside clump	0	2.2	6.5	12	14	9	8	10
Surface	....	....	18	33	33	33	27	17
Station 15 and 16– Spruce-tamarack association								
Air	6.6	14.4	10.5	23	26	20	15	19
Soil	5.5	11	8	15	21	14.5	12	16
Surface	5.5	10	8	28	28	22	27	19
Station 17–Emergent vegetation								
Air	....	....	....	10.5	13	17	17	14
Station 18–Salix associes								
Air	....	....	5.5	8	16	8	12.5	21
Soil	....	....	12	12	8	7	11.5	10
In sun	....	....	19	26	24	9	28	34
Station 19–Arenaria associes								
Air	....	....	....	21	26	9	13.5	20
Sand	....	....	....	23	22	18	13	20
Surface	....	....	....	29	33	22	16	21
Station 20–Agropyron-Draba associes								
Air	....	....	....	18	26	10.5	15	19.5
Soil	....	....	....	17.5	20	18	15	20
Surface	....	....	....	29	33	20	24	20.5
Station 21-Cerastium-Draba associes								
Air	....	....	....	18	26	11	14	19.5
Soil	....	....	....	17.5	20	16	12	19
Surface	....	....	....	29	33	24	20	19.5
Average								
Air	7.2	12	11.6	15.3	20	15.4	13.6	15.4
Soil	5	7.4	9.8	12.1	15	12.2	11.3	13
Surface	9.7	14.2	18	23.3	23	23	23	22

often as great as 22° C. indicating the insulation of lower levels by the sphagnum. Insects behind rocks or within the small clumps of black spruce associated with rocks on the tundra were subjected to very different temperatures from those away from these sites. So great was this variation that early in the season snow remained within these black spruce clumps, while the air temperature outside was 12° C. Table 4 lists the temperatures recorded for all the terrestrial stations.

DESCRIPTION OF HABITATS AND SUCCESSION ON THE TUNDRA

Plant succession on the tundra in this area apparently follows several lines of development to the climax tundra condition. Aquatic and terrestrial habitats are so closely linked that one blends into the other with only a slight change of topography. Permanent pools and lakes maintain themselves through wave action and have abrupt non-eroding banks.

Station 1 (Fig. 3) was at a man-made pool within the environs of Churchill itself. It was four or five feet deep at its deepest point, but was generally shallow enough to wade in. Probably because of pollution, its surface was covered by algae. At one end there were no dikes to retain it, and here sedges and emergent vegetation entered the water. This linked directly with the mixed tundra.

Station 2 was situated on low ground amid dwarf arctic willows *(Salix glauca)* and dwarf birch *(Betula glandulosa)*. This habitat flooded with each rain, but became dry toward the end of the season.

Station 3 was in what may be termed the mixed tundra (Fig. 5). The bulk of tundra area, except that high on hills, is of this type. It is hummocky and water-soaked. Each hummock bears reindeer moss and flowering plants, and among the hummocks are small low areas dominated by sedges and occasional dwarf willow. Shelford and Twomey (1941) refer to this as late sub-climax.

Station 4 (Fig. 4) was in an area of about half an acre, inundated most of the time, and dominated by cotton grass or sedges (*Eriophorum* sp.). In the succession here Station 4 precedes Station 2 which leads directly into Station 3.

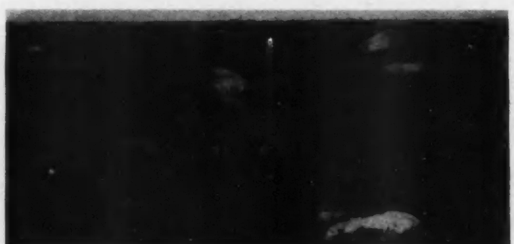

FIG. 5. Station 3, mixed tundra, with Astragalus in full bloom. This is Shelford and Twomey's late subclimax.

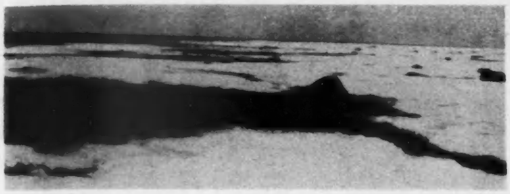

FIG. 6. Churchill Bay tide flats in June. This was Station 12 after the ice melted. Note glacial-deposited rocks.

Station 5 was on a southern slope of the high granite hills along the shores of Hudson Bay. This was the true high climax tundra made more luxuriant in flowering plants because of its greater warmth. It was dominated by at least three genera of reindeer mosses (Cetronia, Usnea, and Oodonia).

Station 6 was at an exposed rock covered with black lichen (*Parmelia* sp.) and surrounded by cranberry plants *(Vaccinum vitisideae),* and was directly above Station 5. This was the same species of cranberry that Seifriz (1926) found in Alpine meadows of the Caucasus Mountains, and on tundra of Russian Lapland.

Station 7 was located in the exposed high climax tundra on the top of the granite uplifts (Fig. 9). Here the sphagnum layer was shallow and soil and air temperatures were cold from constant winds blowing off Hudson Bay. Reindeer moss dominated the area and flowering plants were fewer than in

FIG. 7. Rock-bound coast of Hudson Bay piled high with ice in June. Ice and water action prevent development of lichens on the rocks.

the mixed tundra. Among these were the crowberry *(Empetrum nigrum)* found in both the Caucasian Mountains and Russian Lapland as well as North America (Seifriz 1934). Only occasional clumps of black spruce *(Picea mariana)* grew beside isolated rocks and these were subject to such cold winds that they bore no limbs on their northern exposures. In this area succession followed from bare rock through cranberries, such as at Station 6, through the more luxuriant Station 5 to the bare Station 7 (Fig. 23).

Station 8 was a permanent pool on the high tundra (Fig. 15). It was several feet deep, about an acre in extent, and had abrupt non-eroding banks. Almost no emergent vegetation grew from it, and tundra plants grew to its edge.

Station 9 was a temporary pool among bare rocks of the high tundra (Fig. 14). It contained clear water, was surrounded by lichen-incrusted rocks, and bore no macroscopic plant life.

Station 10 was a pool, probably temporary in some years and permanent during others such as 1936. It was about three feet deep and was on the high tundra a few yards from Stations 8 and 9. It

FIG. 8. Station 13, isolated clump of black spruce. This type of micro-habitat supported a heavy spider population.

was grown up with considerable emergent vegetation, and had a fauna different from that of the other pools. Succession here was probably from Station 9 through Station 10 to the high tundra, or from Station 9 through 10 to the more permanent Station 8.

Station 11 was situated at the edge of a small lake called Lake Annabelle (Fig. 13), about two miles southeast of Churchill, and was one of a series of lakes draining to the south which served as reservoirs for Churchill's water supply. It was, to all appearances, natural and unpolluted. Being large enough to have some wave action, its banks were abrupt and only very slightly eroded where the water undercut the sphagnum. Its southern shores were densely grown up with dwarf arctic willow which served as Station 18. This band of willows was only

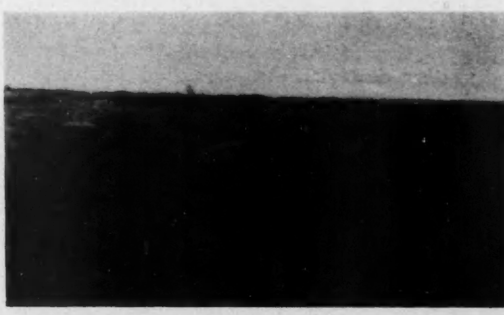

FIG. 9. High tundra, Station 7. Note the mottled appearance of the vegetation mat and the clump of spruces in center background.

FIG. 10. Station 19, the sandwort, *Arenaria peploides*, invading the beach of Hudson Bay.

about a yard or two wide and gave way directly to mixed tundra.

Station 12 was on the tide flat of Churchill Bay (Fig. 6). Because of high tides and the shallow nature of the bay, water flowed inland over a mile between high and low tides. For the first few weeks of observation this area was filled with broken ice and was not studied. After the ice melted, it was found that the regularly inundated area was dominated by grasses. Above these grasses was an extensive region of arctic willow a hundred yards or so in depth. This gave way directly to mixed tundra.

FIG. 11. Station 20, Agropyron-Draba associes on sand. This is the Elymus associes of Shelford and Twomey.

Station 13 was a small clump of black spruce growing beside a large rock out on the mixed tundra (Fig. 8). Such a habitat contained its own fauna and weather conditions, there being a distinct difference between the air temperature outside the clump and inside, and the soil temperature outside and inside. These clumps were but fragments of the black spruce-tamarack forest farther inland and gave way directly to mixed tundra plants.

Station 14 was a small temporary pool in between hummocks near Station 3, and quickly dried up during normal years. It was soon grown up with grass and sedges, but had a fauna different from that of other pools.

Stations 15 and 16 were within the black spruce-tamarack *(Picea mariana-Larix laricina)* forest three miles southeast of Churchill (Fig. 16). The area was inundated during June and, because of the inundation and the hummocky condition of the soil, similar to that of the tundra, tamarack grew in the hollows and black spruce grew on the drier knolls. Station 15 was the layer society of the trees, Station 16 the herb and bush society. Undergrowth beneath the sparsely spaced trees was made up of dwarf willow, flowering plants, and grasses. Tundra lichens invaded the bush and covered the soil. Succession in this area of black spruce-tamarack forest is affected by the edaphic conditions so that it passes from bush to tundra in one area, and from tundra to bush in another. A reduction in the average air temperature would force the trees southward and increase the

FIG. 12. The emergent vegetation of Pool Station 17. Frogs and fish were present in this habitat.

extent of the tundra, and, similarly, reduction of air temperature by exposure increases the tundra invasion. With the presence of isolated clumps of black spruce throughout the tundra in this region, a slight increase in temperature would bring a rapid northward extension of the bush.

Station 17 was another aquatic station. It was at a pool through which a small stream flowed, draining mixed tundra. This pool contained the largest amount of emergent vegetation of any of the aquatic areas under observation (Fig. 12).

Between the outcroppings of granite (Fig. 7) along the shores of Hudson Bay were gravel and sand beaches. Station 19 was on one of these beaches and was in the area of pure sand, littered with driftwood, and bearing patches of sandwort, *Arenaria peploides* (Fig. 10).

FIG. 13. Lake Annabelle showing the dwarf willow border. The lake was Station 11, these willows Station 18.

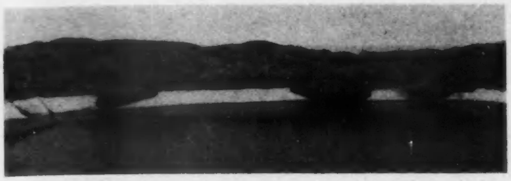

FIG. 14. Pool Station 9 among lichen-encrusted rocks on high tundra.

Above Station 19 was Station 20, in an area of grass-dominated sand plants which had many flowers and an abundant insect fauna (Fig. 11). Farther up the beach Station 20 blended into Station 21, which was the tundra dominated by flowering plants. This in turn gave way to mixed tundra.

From this it will be seen that all habitats in the Churchill area followed lines of succession leading to mixed or high tundra, or farther inland, to the black spruce-tamarack forest. Figure 23 illustrates this.

PLANTS AND THEIR ASPECTION

Plants from this region of Canada include species widely distributed throughout the arctic and subarctic, as well as on alpine meadows. Francis Harper (1931) noted Labrador tea *(Ledum palustris)*, cranberry, wild rosemary, and others in the Athabaska and Great Slave Lake region on the Tazin Highlands. *Dryas integrifolia*, Salix, Saxifraga, and reindeer mosses, according to Davis (1936), were characteristic plants of Akpatok Island in Ungava Bay

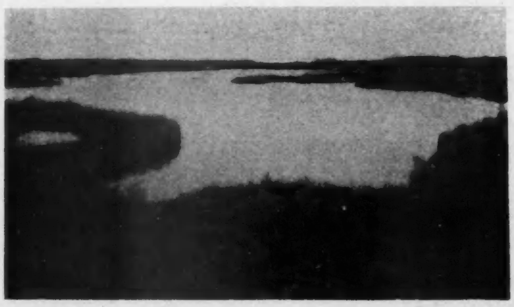

FIG. 15. Pool Station 8 on the high tundra.

at about the same latitude as Churchill. Davis also took many of the same species of insects as were collected at Churchill. Especially were the species of Collembola similar. Charles Elton in Norwegian Lapland (1932) and Seifriz in Russian Lapland both found many species of plants that were taken at Churchill.

Reindeer mosses were of several shades of gray, green, and brown, and upon death turned to a dark brown or black. Since they were interspersed in clumps intermingled with green flowering plants and gray-green dwarf willows, the tundra presented a mottled appearance. This mottled coloration made it very difficult to distinguish objects at any distance.

During the short spring, summer, and fall, plant life, which is abundant in species, produced an amazing array of flowers. Collections were made as each species flowered so as to determine the seasonal aspection. Table 5 lists the plant species taken and the habitats in which each plant was commonly found are indicated.

The first species to bloom was the mountain saxifrage *(Saxifraga oppositefolia)*, which had beautiful lavender flowers. It was abundant along the southern slopes of the granite bluffs. It began blooming about the sixteenth of June and lasted for a week. After it passed its peak of bloom, the large white composite sweet coltsfoot *(Petasites sagittatus)* began blooming along streams and ditch sides. By July 15 it had fruited and was gone. While Petasites was at its heighth of bloom about June 22,

FIG. 16. Stations 15 and 16, the black spruce-tamarack forest association near Churchill. This habitat supported numerous dragonflies, horseflies, and spiders.

white rhododendron, or Lapland rosebay *(Rhododendron lapponicum)* began to flower. A week later it was past full bloom and the arctic heather *(Dryas* spp.), a beautiful three-inch white blossom with orange center, began to bloom. This little flower stood only about four inches high, and completely covered the tundra in some areas. By July 20 Dryas was fruiting, and the purple, white, and light lavender vetches (*Oxytropis* spp. and *Astragalus* spp.)

FIG. 17. Male semipalmated sandpiper on nest in latter part of June. Note clump of Elymus behind the bird and the dense vegetation mat made up of lichens and Dryas plants.

TABLE 5. List of common plant species taken at Churchill, Manitoba.

Group	Species	Common Name	Usual Habitat
THALLOPHYTA			
ALGAE			
	Pediastrum sp.		Fresh-water pools
	Scenedesmus sp.		Fresh-water pools
	Merismopedia sp.		Fresh-water pools
	Glaucocystis sp.		Fresh-water pools
	Fucus vesiculosus L.	Seaweed	Shore of Hudson Bay
LICHENS			
	Parmelia sp.	Lichen	Rocks
	Cetronia sp.	Reindeer moss	Tundra and bush
	Usnea sp.	Reindeer moss	Tundra and bush
	Oodonia sp.	Reindeer moss	Tundra and bush
FUNGI			
	Calvatia cretacea (Berk.) Lloyd	Puffball	Sand, high tundra
	Morchella conicum (Pers.)	Mushroom	High tundra
	Lenzites saepiaria (Wulf.) Fr.	Shelf fungus	Spruce logs in bush
	Psilocybe sp.	Fungus	Wet tundra
PTERIDOPHYTA			
EQUISETACEAE			
	Equisetum arvense L.	Horsetail	Streamsides, bush
SPERMATOPHYTA			
PINACEAE			
	Larix laricina (DuRoi)	Tamarack	Bush
	Picea mariana (Mill.)	Black spruce	Bush, tundra clumps
GRAMINAE			
	Agropyron dasystachum (Hook)	Grass	Sand
	Poa eminens (J. S. Presl.)	Meadow grass	Mixed tundra
	Poa triflora (Grlib.)	Fowl meadow grass	Bush
	Trisetum spicatum (L.)	Grass	Mixed tundra
CYPERACEAE			
	Eriophorum capitatum L.	Cotton grass	Wet tundra
	Eriophorum vaginatum L.	Cotton grass	Wet tundra
ORCHIDACEAE			
	Habenaria obtusata (Pursh.) Richards	Rein orchis	Bush
	Habenaria hyperborea (l.) R. Br.	Orchid	Bush
	Habenaria sp.	Orchid	Bush, high tundra, mixed tundra
SALICACEAE			
	Salix glauca L.	Arctic willow	Bush, wet tundra, Willow flats
POLYGONACEAE			
	Polygonum viviparum L.	Knot weed	High tundra
	Rumex occidentalis Wats.	Sorrel	Incidental
CARYOPHYLLACEAE			
	Cerastium alpinum L.	Alpine chickweed	Sand, high tundra
	Cerastium vulgatum L.	Common chickweed	High tundra
	Arenaria peploides L.	Sandwort	Sand beaches
	Stellaria sp.	Starwort	Incidental
	Viscaria sp.		High tundra
RANUNCULACEAE			
	Ranunculus purshii Richards	Buttercup	Sand
	Ranunculus fascicularis Muhl.	Early crowfoot	Wet tundra
	Ranunculus sp.		High tundra
	Caltha palustris L.	Marsh marigold	Streamsides
	Anemone richardsonii Hook	Anemone	Lake edge
	Batrachium divaricatum (Schrank) Wimmer	Aquatic buttercup	Pool 1
CRUCIFERAE			
	Lesquerella sp.		Incidental
	Lesquerella arctica (D. C.) Watts		High tundra
	Draba arabisans (Michx.)		Sand, incidenta
	Draba incana L.		Sand, mixed tundra
	Cardamine pratensis L.	Cuckoo flower	Wet tundra
	Brassica sp.	Mustard	Sand
SAXIFRAGACEAE			
	Saxifraga oppositefolia	Mountain saxifrage	High tundra
	Saxifraga tricuspidata Rottb.		Sand, mixed tundra
	Saxifraga caespitosa L.		Wet high tundra
	Ribes hudsonicus Richards	Gooseberry	Incidental
	Ribes setosum Lindl.	Gooseberry	Incidental
	Parnassia palustre L.	Grass of Parnassia	Bush
ROSACEAE			
	Rubus chamemorus L.	Cloudberry	High, mixed tundra
	Rubus arcticus L.	Arctic dewberry	Bush
	Potentilla nivea L.	Cinquefoil	Sand
	Potentilla anserina L.	Silverweed	Wet tundra
LEGUMINOSAE			
	Oxytropis sp.	Vetch	Tundra
	Astragalus crassicarpus Nutt.	Purple milk vetch	Sand
	Astragalus sp.	White milk vetch	High, mixed tundra
	Dalea sp.		Mixed tundra
EMPETRACEAE			
	Empetrum nigrum L.	Crowberry	High tundra
ONAGRACEAE			
	Epilobium lineare L.	Willow herb	Incidental, bush
	Epilobium angustifolium L.	Fireweed	High tundra
	Epilobium latifolium L.	Fireweed	Sand
ERICACEAE			
	Andromeda polifolia L.	Pink bell	Mixed tundra
	Ledum palustre L.	Labrador tea	Bush, high tundra
	Loiseleuria procumbens (L.)	Alpine azalea	Mixed, high tundra
	Rhododendron lapponicum (L.)	Lapland Rose Bay	Hig tundra
	Pyrola minor L.	Wintergreen	High tundra
	Pyrola uliginosa Torr.	Wintergreen	High, mixed tundra
	Arctostaphylos alpina (L.) Spreng.	Alpine bearberry	High, mixed tundra
	Vaccinium vitis-ideae L. variety *minus* Ladd.	Cranberry	High tundra
	Dryas integrifolia Vahl.	Arctic heather	Tundra
	Dryas octopetala L.	Arctic heather	Tundra
	Shepherdia canadensis L.		High tundra
PRIMULACEAE			
	Androsace diffusa Small		Incidental, sand
	Primula egalikseensis Wormsk.	Primrose	Wet high tundra
	Primula mistassinica	Primrose	Tide flat
BORAGINACEAE			
	Mertensia lanceolata (Pursh.)	Lungwort	Sand
	Lappula texana Britton	Stickweed	Sand
	Myosotis sp.	Forget-me-not	Incidental
VERBENACEAE			
	Verbena sp.	Vervain	Bush
SCROPHULARIACEAE			
	Pedicularis lapponica L.	Lousewort	Mixed tundra
	Pedicularis groenlandica Retz.		Mixed tundra
	Pedicularis sp.		Mixed tundra
	Castilleja coccinea (L.) Spreng.	Painted cup	Mixed tundra, bush
LENTIBULARIACEAE			
	Pinquicula vulgaris L.	Butterwort	Incidental
COMPOSITAE			
	Petasites sagittatus (Pursh.) Gray	Sweet coltsfoot	Streamsides
	Achillea millefolium L.	Common yarrow	Sand, mixed tundra
	Achillea lanulosa Nutt.	Yarrow	Sand
	Taraxacum erythroperum Andrz.	Dandelion	Sand
	Chrysanthemum arcticus L.	Oxeye daisy	Wet tundra

were well started toward full bloom. During this time, orange, yellow, and purple *Pedicularis* spp. were blooming, and they began fruiting by July 20.

The first plant to invade the sand beaches of Hudson Bay was the sandwort *(Arenaria peploides)* which began to bloom toward the end of June. By July 16 it was past bloom and fruiting. Early in July cotton grasses (*Eriophorum* spp.) came into fruit and where they were dominant in the swampy areas, the tundra looked like a cotton plantation. By July 20 cotton grass, willows, and knotweed *(Polygonum viviparum)* were in full flower. A small, pink, bell-like flower, which the natives called the arctic rosemary *(Andromeda polifolia)* had begun to bloom by July 15, while at this time cranberry was in full flower. By July 21 light green and purple orchids (*Habenaria* spp.) were past full bloom, and marsh marigold *(Caltha palustris)* was in full sway over the streamsides. Common yarrow *(Achillea millefolium)* was an abundant plant of the high sand beaches, and it began to bloom in the middle of July. During the week of July 20 fireweed (*Epilobium* spp.), yarrow, white daisies (*Chrysanthemum* sp.), and wintergreen (*Pyrola* spp.) came into full bloom. By July 20 most of the other small flowers were past blooming. Fireweed and Indian paint brush *(Castilleja coccinea)* became the dominant color background during the last week of July. The last flower to bloom before the observations were closed was a little aquatic buttercup *(Batrachium divaricatum)*, which bloomed under the water in Pool 1.

A number of these plant species are apparently circumpolar in distribution. Seifriz (1934) found the following in Russian Lapland 750 miles north of Leningrad: *Rubus chamaemorus, Vaccinium vitis-idaea, Ledum palustre, Empetrum nigrum, Epilobium angustifolium, Loiseleuria procumbens, Andromeda polifolia, Saxifraga oppositefolia, Pedicularis lapponica, Dryas octopetala, Eriophorum vaginatum, Caltha palustris, Parnassia palustris,* and *Achillea millefolium.*

Further information concerning flower aspection is shown in Figure 22. In this figure the approximate date of the beginning of flowering is shown for each species.

INVERTEBRATES FROM THE REGION OF CHURCHILL, MANITOBA

The fauna of the tundra, especially in this region, is far more abundant than would be ordinarily anticipated. Animal life was extensive both in number of species and in individuals. Among some of the groups collected there were new species, and many that were related more closely to European forms than to American forms. In many ways, the tundra invertebrates of North America show a direct relationship to those of Europe and Asia, especially as some species are circumpolar. Invertebrates from Churchill vicinity and the habitats in which they were found were as follows:

PLATYHELMINTHES

Typhloplanidae:

In almost every permanent and many temporary pools was the small brownish rhabdocoel *Mesostoma arctica* Hyman. This proved to be a new species and was described by Miss Hyman (1938). It swam swiftly about among the detritus and plants of pools, and, when sexually mature, contained bright reddish-purple eggs which were visible from above.

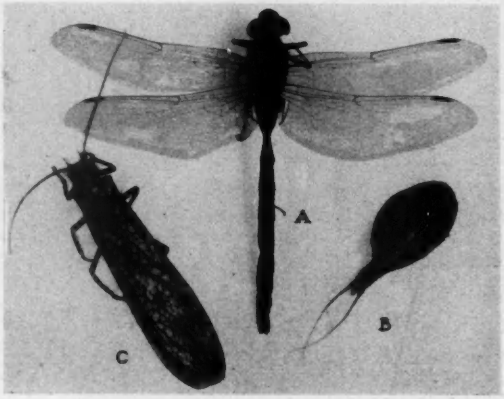

FIG. 18. Slightly reduced. A, common dragonfly, *Aeshna juncea americana,* of the black spruce-tamarack forest; B, *Lepidurus arcticus,* a crustacean found in Pool Station 1; C, *Pteronarcys shelfordi,* a stonefly common in Churchill River.

ANNELIDA

Hirudinea:

Placobdella phalera Graf. found in permanent pools.

Lumbricidae:

Lumbriculus sp. found in temporary and permanent pools.

MOLLUSCA

Aplexa hypnorum (L.), in temporary pools; *Stagnicola palustris nuttaliana* (Lea.) in permanent pools; *Gyraulus circumstriatus* (Tyron.) noted by Dr. F. C. Baker to be the farthest north as yet reported; *Physa* sp. in permanent and temporary pools; *Euconulus fulvus* (Müller) found under loose bark of spruce logs in the bush; *Succinea grosvenori* (Lea.) in wet tundra; and *Vertigo ventricosa* (Say) in tundra surface sphagnum.

ARTHROPODA

CRUSTACEA

Anostraca:

In all of the fresh-water pools, except very temporary ones such as Station 14, *Branchinecta paludosa* (Müller) was the only species present.

Notostraca:

Lepidurus arcticus found only in permanent pool, Station 1 (Fig. 18-B).

Cladocera:

Daphnia pulex (De Geer) commonest species in permanent and temporary pools; *Daphnia magna* Straus, reported by Dr. Chancey Juday to be its farthest north in Canada, although found in Greenland, and present in temporary and permanent pools; *Eurycercus lamellatus* (O. F. Müller) and *Simocephalus vetulus* (O. F. Müller) in permanent and temporary pools.

Amphipoda:

Gammarus locusta (L.) found along shores of Hudson's Bay. When tide was receding this species swam rapidly out with the current, numbering as high as 200 individuals per square foot. It is circumpolar in distribution.

Copepoda:

Heterocope septentrionalis in temporary and permanent pools; *Diaptomus arcticus* (L.) in temporary and permanent pools; *Diaptomus tyrrelli* Poppe in permanent pools; *Cyclops vernalis* in temporary pools.

ENTOMOSTRACA

OSTRACODA

Cypridae:

Eucypris crassoides Alm., *Cyclocypris globosa ovoides* Alm., and *Candona candida* (O. F. Müller) from permanent pools.

ARACHNIDA

Neobisiidae:

According to Dr. J. C. Chamberlin, the species of *Microbisium* near *brunneum* (Hogen) taken on soil of tundra was the first of the Microbisium genus taken in Canada.

Hydracarina:

Pionacereus sp. and *Piona nodata latigenitalis* Mar. in permanent pool, Station 1; *Thyas stolli* Koen., *Acercus* sp., and *Lebertia setosa* Koen. in temporary pools.

Acarina:

Over 1600 specimens of terrestrial forms were taken in sphagnum samples. Many new species were represented and have as yet not been described.

Eupodidae:

Tydeus sp. from mixed tundra; *Norneria* sp. from mixed tundra and high climax tundra; *Penthaleus* sp. from sphagnum of willow-birch habitat.

Bdellidae:

Bdella semiscuta S. Thor. from high and low tundra; *Bdella* sp. from high tundra; *Cyta* sp. distributed over tundra; *Cyta latirostris* (Herm.) from high climax tundra; *Scirus* sp. near *magnus*, a brilliant red species prolific under decaying kelp of shores of Hudson's Bay and predacious on small insects and fly larvae in the kelp.

Trombidoidea:

Belaustium sp. common over tundra; *Microtrombidium sucidum* Koch found in mixed tundra and willow habitats. *Bryobia* sp. near *brevicornis* Ewing common over tundra; and *Bryobia* sp. over tundra.

Raphignathidae:

Raphignathus parrius Berlese from mixed tundra.

Parasitoidea:

Seiulus (Lasioseius) sp. common over tundra.

Oribatoidea:

Dameosoma sp. from mixed tundra; *Suctobelba* sp. over tundra; *Hypocthonius* sp. from mixed tundra; *Nothrus* sp., *Nothrus horridus* (Herm.), and *Microzetes* sp. common over tundra.

Feather mites were found on many birds including: *Avenzoaria calidridis* Oud. on red-backed sandpiper *(Pelidna alpina sakhalina)*, sanderling *(Calidris leucophaea)*, stilt sandpiper *(Micropalama himantopus)*; *Avenzoaria* sp. on Hudsonian curlew *(Numenius hudsonicus)*; *Analges tyranni* L. on Canada jay *(Perisoreus canadensis canadensis)*; *Analges passerinus* L. on Lapland longspur *(Calcarius lapponicus lapponicus)*, Harris' sparrow *(Zonotrichia querula)*, redpoll *(Acanthis linaria linaria)*, hoary redpoll (*Acanthis* sp.), American pipit *(Anthus rubescens)*, snow bunting *(Plectrophenax nivalis nivalis)*, tree sparrow *(Spizella monticola monticola)*, northern horned lark *(Otocoris alpestris alpestris)*, white crowned sparrow *(Zonotrichia leucophrys)*; *Analges* sp. on squaw duck *(Harelda hyemalis)*; *Proctophyllodes truncatus* Robin. on Lapland longspur, Smith's longspur *(Calcarius pictus)*, snowbird, tree sparrow, hoary redpoll, horned lark, savannah sparrow *(Passerculus sandwichensis savanna)*, and white crowned sparrow; *Alloptes* sp. on Hudsonian godwit *(Limosa haemastica)*; *Pterolichus buchholzi* Can. var. *fascigera* Megn. and Tr. on herring gull *(Larus argentatus)*, turnstone *(Arenaria interpres)*, and golden plover *(Charadrius dominicus dominicus)*; *Pterolichus charadrii* (Can.) on semipalmated plover *(Aegialitis semipalmata)* (Fig. 17), and eastern dowitcher *(Macrorhampus griseus)*; *Megninia oscinum* (K.) Berl. on tree sparrow and white-crowned sparrow; *Pteronyssus puffini* Buchh. on parasitic jaeger *(Stercorarius parasitica)*.

ARANEIDA

Dictynidae:

Dictyna sublata (Hentz) from bush; *Dictyna volucripes* Keyserling from spruce clumps; *Dictyna muraria* Em., *D. vincens* Chamb., and *Argenna* sp. from tundra plants.

Lycosidae:

The lycosid *Pardosa groenlandica* (Thorell) was the most prevalent and conspicuous inhabitant of the sand beaches of Hudson's Bay between the tidal area and the area dominated by *Arenaria peploides*. During July females dragged behind them their cocoons of eggs which hatched the first of August. *Pardosa* sp. was found on tundra sod surface; *Pardosa mackenziara* (Keyserling) from bush; *Pardosa concinna* (Th.) (Fig. 20C) from high tundra; *Lycosa* sp. from mixed tundra.

Myeryphantidae:

Hypselistes florens (Cambridge) from bush; *Euliara tigana* Cham. and Ivie., *Erigone tentigera* (Cambridge), *Grammonata inornata* Emerton, *Cornicularia communis* Emerton, *Cornicularia* sp., and *Mantilaira* sp. from dwarf willows; *Spiropalpus spiralis* Emerton from mixed tundra; *Oedothorax* sp. from wet tundra.

FIG. 19. One of the common chironomids resting on a twig. Enlarged.

Linyphidae:

Pityohyphantes phrygiana (C. Koch) and *Bathyphantes* from bush; *Pityohyphantes limitanea* Emerton from spruce clumps; *Microneta* sp. from dwarf willows.

Argiopidae:

Tetragnatha extensa (Linn.) from both tundra and bush and found by Shelford (1935) to be subclimax influents in the coniferous forest farther south. *Zilla* sp. from bush, and *Araneus patagiatus* Clerck. from both tundra and bush.

Thomisidae:

Xysticus bimaculatus Emerton from beach plants; *Oxyptilia* sp. from dwarf willow; *Philodromus* sp. from bush; and *Ebo pepinensis* Gertsch from spruce clumps.

Clubionidae:

Clubiona sp. from tundra and bush.

Salticidae:

Phidippus sp. from dwarf willow.

HEXAPODA

COLLEMBOLA

Poduridae:

Podura aquatica L. from wet tundra; *Achorutes armatus* Nicolet, *Micranurida pygmaea* Borner and *Anurophorus laricis* Nicolet from tundra mat; *Achorutes pseudoarmatus* Folsom found on surface of pools; *Onychiurus groenlandicus* Tullberg from low tundra mat; *Friesea mirabilis* Tullberg and *Isotoma bipunctata* Axelson, stated by Dr. H. B. Mills to have not been recorded from western hemisphere before, found in tundra mat; *Tetracanthella* sp. from high tundra mat; *Folsomia fimetaria* L., *F. diplophthalma* Axelson, *F. quadrioculata* Tullberg, *F. elongata* MacGillivary, *Isotoma olivacea* Tullberg, and *I. viridis* Bourlet from tundra mat; *Isotomurus palustris* Müller from low tundra; and *Isotomurus retardatus* Folsom found on surface of temporary pools.

Entomobryiidae:

Entomobrya nivalis L. and *Entomobrya* sp. near *muscorum* Tullberg from tundra mat.

Sminthuridae:

Sminthurides pumilis Krausbauer, *S. occultus* Mills, *Arrhopalites* sp., and *Deuterosminthurus insignis* (Reuter) from low tundra mat.

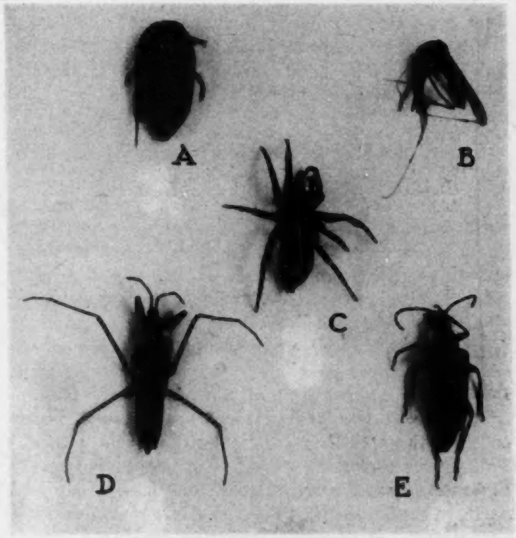

FIG. 20. Three times natural size. A, common water beetle, *Agabus arcticus*, found in all of the fresh-water pools; B, mosquito, *Aedes nearcticus;* C, running spider, *Pardosa concinna*, common on the high tundra; D, water strider, *Gerris pingreensis*, found on most of the pools, especially at Station 17; E, a cerambycid, *Acmaeops pratensis*, which commonly fed on pollen in the flowers of the tundra.

ORTHOPTERA

Locustidae:

Acrydium sublatum (L.) from tundra; *Melanoplus borealis borealis* (Fisher) abundant in bush along railroad right-of-way.

EPHEMERIDA

Baetidae:

Baetis brunneicolor McD. and *B. hudsonicus* Ide found along edges of larger lakes; *B. hudsonicus* described by Dr. F. P. Ide in 1937.

ODONATA

Aeschnidae:

Aeshna juncea americana Bart. (Fig. 18A), *A. sitchensis* Hagen, *A. coerulea septentrionalis* Hagen, and *A. eremita* Scudder abundant in bush feeding on *Simulium* spp. and *Aedes* spp.

Cordulidae:

Somatochlora albicincta Burm. and *S. whitehousi* Walker common in bush.

Coenagrionidae:

Coenagrion resolutum Hagen found breeding and developing in numbers at permanent pool, Station 17.

Plecoptera:

Plecoptera developed in abundance in lakes and Churchill River. During their heavy flights they could be collected resting on sides of buildings at Churchill. Most species taken have not yet been identified.

Pteronarcidae:

Pteronarcys shelfordi Frison, a large and beautiful species (Fig. 18C) rarely seen and apparently developing in the Churchill River.

Mallophaga:

Several hundred specimens were taken from birds, but the identification of these is incomplete.

Menopon infrequens Kell. found on Bonapartes Gull *(Larus philadelphia)*; *Ricinus clypeatus* Mjb. on northern horned lark; *Gonoides lagopi* L. found on willow ptarmigan *(Lagopus lagopus lagopus)*; *Lagopoecus protervus* Kell. on willow ptarmigan; *Anatoecus dentatus* Scopoli on greater scaup duck *(Nyroca marila)* and lesser scaup duck *(Nyroca affinis)*; *Philopterus gonothorax* Giebel on herring gull; *Philopterus jungens* Kell. on northern flicker *(Colaptes auratus lutens)*; *Philopterus colymbinus* Denny on black-throated loon (arctic loon) *(Gavia arctica)*; *Philopterus melanocephalus* N. on parasitic jaeger; *Philopterus subflavescens* Geoff. on Canada jay and northern water thrush *(Seiurus noveboracensis noveboracensis)*; *Degeeriella euprepes* Kell. and Chapman on ruddy turnstone; *Degeeriella fusca* N. on eastern sparrow hawk *(Falco sparverius sparverius)*; *Degeeriella normifer* Grube on parasitic jaeger; *Degeeriella ornata* Grube on Bonapartes gull; *Esthiopterum crassicorne* Scop. on greater scaup duck and American golden eye *(Clangula clangula americana)*.

THYSANOPTERA

Aeolothripidae:

Aeolothrips fasciatus (L.) from flowers on sand beaches.

Thripidae:

Thrips sp. near *madroni* Mault from tundra flowers including *Petasites sagittatus* and from dwarf willows; *Thrips tabaci* Lind. from plants on sand beaches; *Taeniothrips vulgatissimus* Hal. from tundra flowers; *Aptinothrips rufus* (Gmelin) from plants on sand and on river tide flats; *Anaphothrips* sp. from plants of river tide flats; *Chirothrips manicatus* Hal. from plants of river tide flats and sand; and *Frankliniella tritici* (Fitch) from tundra flowers including *Ledum palustre, Astragalus crassicarpus, Caltha palustris, Petasites sagittatus, Dryas integrifolia,* and *Pedicularis lapponica.*

HEMIPTERA

Corixidae:

Callicorixa noorvikensis Hungerford, *C. alaskensis* Hungerford, *Arctocorixa chancei* Hungerford, and *A. convexa* Fieb. from permanent pools. These species laid their eggs early in June and new adults were appearing the first of August.

Saldidae:

Salda littoralis L. abundant on river tide flats.

Gerridae:

Gerris pingreensis D. and H. (Fig. 20D), and *G. marginatus* Say found only on permanent pool, Station 17.

Miridae:

Lygus pratensis L. found on beach plants; *Nysius* sp. and *Chlamydatus pullus* Reut. common in *Draba-Cerastium* habitat; *Melanotrichus* sp. on river tide flats.

Nabidae:

Nabis limbatus Dahlb. common on flowers on sand beaches.

Anthocoridae:

Teratocoris herbaticus Uhl. common on river tide flats, also found on tundra.

HOMOPTERA

Cicadellidae:

Laevicephalus striatus (L.), *L. asper* (Rib.), and *Strogylocephalus agrestis* (Fall.) common on plants of sand habitats; *Macrosteles* sp. near *sexnotata*, *M. fascifrons* (Stal.), and *M. divisus* (Uhler) common on river tide flats.

Chermidae:

Chermids were the first flying forms taken in the spring. *Psyllia breviata* Patch, *P. fibulata* Crawf., and *Triosa varians* Crawf. abundant on dwarf willows; *Aphalara nigra* Cald. common in clumps of spruce on tundra.

Fulgoridae:

Delphacodes pellucida (Fabr.) and *D.* sp. near *kilmani* on river tide flat plants; *D. albostriata* (Fieb.), *D. campestris* (Van D.), and *Epiptera* sp. on plants of sand beaches.

Aphididae:

Aphis monardae Oestl. found on tundra forget-me-not and *Capitophorus minor* (Forbes) on cloudberry.

Coleoptera:

Dytiscids and hydrophilids were commonest of tundra beetles because of prevalence of aquatic situations. Adults were noted frozen in lake ice early in

June and they mated and laid eggs soon after becoming free of the ice. Their larvae fed upon insects and crustaceans of the pools. When fullgrown they emigrated to sphagnum surrounding the pools. Adults fed extensively on chironomid larvae.

Carabidae:

Dyschirius nigripes Lec. abundant on river tide flats; *Dyschirius* sp. on mixed tundra; *Trichocellus porsildi* Brown on tundra plants; *Bembidion* vic. *longulum* on aquatic plants.

Haliplidae:

Haliplus strigatus Tobt. from temporary and permanent pools.

Dytiscidae:

Colymbetes sculptilis Harr., *Coelambus hudsonicus* Fall, *Coelambus* sp., *Hydroporus lapponum* Gyll., *H. appalachius* Sherm., *H. arcticus* Thom., *Hydroporus* sp. near *striola, Agabus antennatus* Leech, and *Ilybiosoma bifaria* Kirby common in permanent pools; *Agabus colymbus* Leech and *A. infuscatus* Aube in permanent pools of climax high tundra; *Hydroporus griseostriatus* DeG. and *Agabus arcticus* Payk. (Fig. 20A) in lakes; *Hydroporus melanocephalus* Gyll., *H. rufinosus* Mann., *Agabus* sp. near *confertus, A. bicolor* Kby. found in temporary pools; and *Ilybius discedens* Sharp. found in debris on Hudson's Bay beaches. The larva of *Ilybius angustior* Gyll. was reared in captivity and pupated on July 4. The pupa was pure white except for tan eyes, and it was active, squirming vigorously. Five days after pupation the eyes turned black. After eight days the appendages were turning brown at their tips. On July 14 the adults emerged.

Gyrinidae:

Gyrinus minutus L. not common, but on permanent pools.

Hydrophilidae:

Laccobius sp., *Hydrobius fuscipes* L., *Cercyon praetextatum* Say, *Ochthebius holmbergi* Makl., *Helophorus nitidulus* Lec., and *Helophorus* sp. found in temporary pools.

Silphidae:

Silpha lapponica Hbst. and *S. trituberculata* Kirby larvae and adults found on carcasses of birds and mammals.

Staphylinidae:

Stenus umbratilis Casey on plants in permanent pools. *S. retrusus* Casey from wet tundra; *S. occidentalis* Casey, *Stenus* sp., and *Euaesthetus* sp. on plants in temporary pools; *Arpedium* sp. along lake edges in willows.

Cantharidae:

Cantharis mandibularis Kirby on tundra flowers; *Podabrus perplexus* Brown on river tide flat flowers. The larvae of *Podabrus heteronychus* lived in the tundra mat and were predacious on small insects. Reared in captivity, they pupated on June 18. The pupa in its sphagnum cell rested in a curved position and was a creamy yellow and pink. Five days after pupation the wings and eyes turned black. In the next day or so the thorax and head turned black and the tip of abdomen became darkened. The adults emerged on June 25 during the night.

Mordellidae:

Mordella borealis Lec. adults found in tundra flowers and larvae found in fungus *Morchella conicum.*

Pythidae:

Pytho americanus Kirby and *Pytho* sp. in spruce logs of bush.

Elateridae:

Ampedus sp. on sand plants and *Sericus incongruus* Lec. found on dwarf willows.

Buprestidae:

Chrysobothris sp. found in spruce logs.

Helodidae:

Cyphon variabilis Thunb. found in bush.

Byrrhidae:

Byrrhus americanus Lec. on the tundra.

Lathridiidae:

Lathridius cinnamopterus Mann. on plants of permanent pools; *Corticaria dentigera* Lec., *C. ferruginea* Marsh., and *Melanopthalma americana* Mann. among debris on Hudson's Bay beaches.

Anobiidae:

Coenocara scymoides Lec. on mixed tundra.

Scarabeidae:

Aphodius sp. among debris of beaches.

Cerambycidae:

Xylotrechus undulatus Say in spruce logs of bush; *Acmaeops pratensis* Laich in flowers of tundra (Fig. 20E).

Chrysomelidae:

Phyllodecta americana Schffr. in bush and on tundra; *Haltica shoemakeri* Lec. on sand plants; *Phaedon oviformis* Schffr. on sand and tundra plants; *Chrysomela* sp. on sand plants.

Curculionidae:

Dorytomus sp. among dwarf willows.

Trichoptera:

Caddis flies constituted an important fauna of permanent pools and lakes. The several species have not been identified to date. Larvae of these fed on the pool bottoms and migrated during the last of July from the water into the surrounding sphagnum where they pupated. At no time were the adults conspicuous, but they were taken over most of the tundra.

LEPIDOPTERA

Incurvariidae:

Adela sp. on dwarf willows.

Gelechiidae:

Gelechis sp. and *Gnorimoschema* sp. on sand plants.

Plutellidae:

Plutella maculipennis Curtis on sand beach plants.

Tortricidae:

Ancylis sp. found on plants of sand beaches.

Pyralididae:

Crambus sp. on mixed tundra.

Geometridae:

Xanthorhoe ferrugata Clerk found on plants of sand beaches.

Noctuidae:

Autographa sp. in bush. The larvae of *Hillia iris* Zett. fed upon leaves of dwarf willow. They were not in abundance nor were they voracious feeders. Larvae taken on the twenty-ninth of June were full-grown and over an inch long by July 18. During the next two days they dropped to bottom of rearing jar and spun flimsy light brown cocoons. They pupated by July 20 and emerged some time between August 4 and 10. *Graptolitha* sp. found on plants of sand beaches and *Thiodia* sp. taken in spruce clumps on tundra.

Satyridae:

Oeneis melissa semidea (Say) over tundra, a day-flying moth.

Thirteen species of butterflies were conspicuous over the tundra and along streams and railroad right-of-way in the bush. The first species to appear was the brown *Erebia rossii*. They appeared the last of June and first of July, and after them, pierids and nymphalids came in rapid succession. In ratio of numerical abundance over the tundra they appeared between July 10 and 18 as follows:

Hesperidae:

Glaucopsyche lygdamus couperi (Grote) one percent and *Hesperia comma manitoba* Scudder two percent.

Pieridae:

Colias nastes (Bov.) 36 percent, *C. christina* form *gigantea* (Edw.) 18 percent, *C. palaeno chippewa* (Kirby) 19 percent, *C. hecla hecla* (Stkr.) two percent, and *Pieris napi cleracea* Harris one percent.

Nymphalidae:

Erebia rossii Curtis ten percent, *Brenthis frigga saga* (Staudinger) one percent, *B. aphiraphe triclaris* (Hubner) 1.5 percent, *B. charicles* (Schneider) 1.5 percent, *Plebius aquilo* (Bvd.) one percent, and *Cynthia cardui* L. one percent.

Diptera:

Many species undetermined. Most abundant insects of the tundra.

Tipulidae:

Tipula sp. near *appendiculata* Loew from dwarf willows; *Tipula* sp., *Tipula (Yamatotipula)* near *sulpurea* Doanes, *Tipula (Vestiplex)* near *platymera* Walker, *Limonia (Dicranumyia)* sp., and *Nephrotoma altissima erythrophyrs* (Williston) from mixed tundra; *Limnophila (Idioptera) mcclureana* Alex. (1938), *Limnophila* near *poetica* O. S. and *Prionocera* sp. from wet tundra; *Limnophila (Phylidanea)* near *platyphallus* Alex., and *Helobia hybrida* Meigen from bush; *Erioptera* sp. from mixed tundra; *Phalacrocera* near *neoxena* Alex. from vegetation of permanent pools; *Prionocera dimidiata* (Loew) from dwarf willows; and *Tipula (Yamatotipula) kennicotti* Alex. from mixed tundra. Larvae of *Prionocera fuscipennis* (Loew) fed on the bottom of permanent pool, Station 17. By June 22 they had become full-grown and were floating up from the bottom to the surface of the water. There they swished about until their bodies struck emergent vegetation or algae, where they pupated. Captive larvae pupated on June 26 and immediately after ecdysis the pupae were long and white. They soon shortened and turned light brown. Six days later the thorax and wing pads had darkened, and the adults emerged.

Psychodidae:

Pericoma sp. from river tide flats.

Chironomidae:

Species numerous but undetermined (Fig. 19).

Culicidae:

Aedes nearcticus Dyar (Fig. 20B), *A. punctor* Kirby, *A. nigromaculis* Ludlow, *A. alpinus* Linn., and *Aedes* sp. all distributed over tundra and bush.

Mycetophilidae:

Sciara tridentata Rubsaamen, *S. habilis* Joh., *S. prolifica* Felt., *Mycetophila vitrea* Coq., *M. fungorum* DeGeer, *M. scalaris*, *Exechia absolute* Fab., and *Bolitophila* sp. distributed over the tundra and bush.

Cecidomyiidae:

Monardia sp. from river tide flats, *Prionellus* sp. from high climax tundra; *Dasyneura* sp. and *Diplosid* sp. from mixed tundra.

Simuliidae:

Simulium vittatum Zett., and *S. venustum* Say most numerous flies of tundra and bush; *S. corbis* Twinn and *S. subexcisum* Edw. from beach plants.

Tabanidae:

Tabanus zonalis Kirby, *T. rhombicus* O. S., *T. illotus* O. S., *T. affinus* Kirby, *Chrysops carbonarius* Walker, and *C. furcata* Walker common in bush but not abundant over tundra.

Dolichopodidae:

Dolichopus plumipes Scap. from mixed tundra; *Hydrophorus brevicauda* V. D. from climax tundra; and *Scellus spinimamus* Zett. from river tide flats.

Syrphidae:

Melanostoma sp. near *chaetopoda* David and *Eristrophe sodalis* Will. from dwarf willows; *Melanostoma pictipes* Big., *Platycheirus scutatus* Mg., *Platycheirus* sp., and *Sphaerophoria* sp. from mixed tundra flowers; *Sphaerophoria nigratarsi* Fluke from sand flowers; *Helophilus* sp. and *Eristalis* sp. from permanent pools where larvae were found entering pupation during June.

Anthomyiidae:

Hylemya constricta Mall. from mixed tundra; *Spilogona alticola* Mall. from dwarf willows; and

Spilogona setinervis Huck. on emergent vegetation of pools.

Calliphoridae:

Calliphora sp. and *Cynomya cadaverina* Desvoidy (Fig. 21) from animal carcasses.

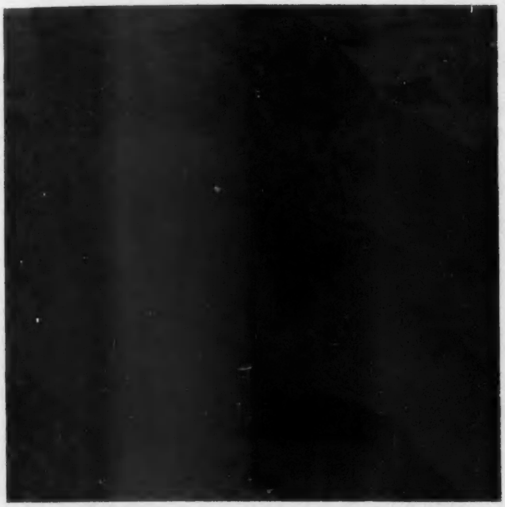

FIG. 21. Blowflies, *Cynomya cadaverina*, resting on a rock.

Muscidae:

Pogonota kincaida Cov. and *Helina nigrita* Mall. from tundra; *Scopeuma furcata* Say, and *S. suila* from dwarf willows; *Scopeuma nigripes* Holm. from tundra flowers.

SIPHONAPTERA

Ceratophillidae:

Ceratophyllus garei Roths. from willow ptarmigan *(Lagopus lagopus)*, Harris' sparrow, Smith's longspur, and white-crowned sparrow; *Monopsyllus vison* (Bak.), *M. eumolpi* (Roths.), and *Monopsyllus* sp. from Hudsonian red squirrel *(Sciurus hudsonicus)*.

HYMENOPTERA

Tenthridinidae:

Several species were common throughout the tundra, especially associated with willow thickets and spruce forest, but they have as yet not been determined.

Braconidae:

The number of species of parasitic Hymenoptera was great and they were present in all types of terrestrial habitats. Identification of these beyond genus was nearly impossible because of lack of associated host relationships.

Ichneutes sp., *Meteorus dimidiatus* Cresson, *Pentapleura* sp., *Aphidius* sp., *Euphorus pallipes* Curtis, and *Proterops* sp. were taken among arctic willows; *Microbracon* sp., *Adelius* sp., and *Epiclista* sp. from low wet tundra; *Microbracon gelechiae* (Ashm.) *Meteorus* sp., and *Orgilus* sp. from mixed tundra; *Apanteles* sp., *Microgaster* sp., *Leiophron laevis* Cress., *Chelonus* sp., *Adialytus* sp., and *Bracon solidaginis* Vierick from tundra flowers; *Meteorus vulgaris* Cresson from isolated spruce clumps; and *Aspilota* sp. from the bush.

Alysiidae:

Chorebus sp. taken from beach habitats; *Alysia* sp., *Mesocrina* sp., and *Isomerista* sp. from willows; *Dinotrema* sp. from isolated spruce clumps; *Rhizarcha* sp. and *Dacnusa* sp. from tundra flowers; and *Aphanta* sp. from the emergent vegetation of pool, Station 17.

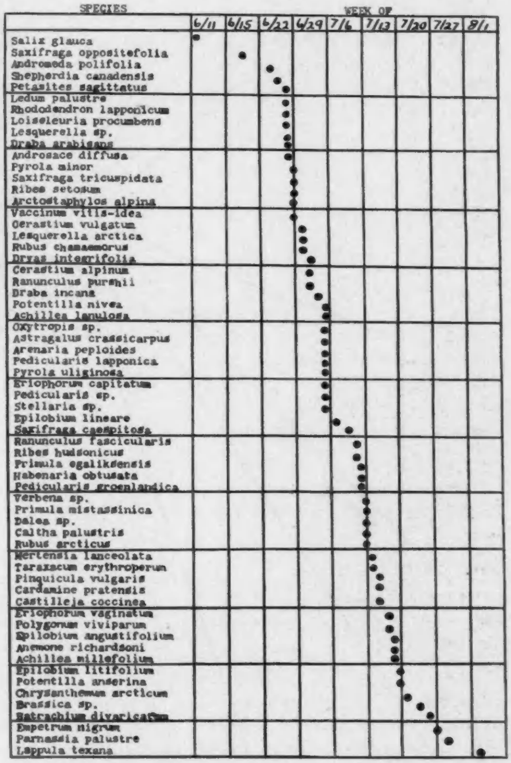

FIG. 22. The flower aspection of plants at Churchill, Manitoba. Each spot indicates the date when first blooms were noted.

Ichneumonidae:

Cryptus sp., *Eclytus* sp., *Mesochorus* sp., *Zootrephes compressiventrus* (Cresson), *Homelys* sp., *Pammicra* sp., *Gausocentrus* sp., *Exochus curvator* Fabr., *Isadelphus* sp., *Meniscus* sp., and *Endasys* sp. from tundra flowers; *Epiurus* near *bicoloripes* (Ashm.), *Gelis* sp., *Zaplethocornia* sp., *Phaeogenes gaspesianus* Prov., *Aclastus* sp., *Monoblastus* sp., *Campoplex* sp., *Hemimachus* sp., *Callidiotes* sp., and *Pimpla* sp. from dwarf willows; *Syrphoctonus minimus* (Cresson), *Habromma* sp., and *Bathymetis* sp. from the river tide flats; *Phygadeuon* sp. from mixed tundra; *Exoclytus* sp., *Stenomacrus* sp., *Pezoporus* sp.,

Symplecis sp., *Scopesis* sp., *Zaphleges* sp., *Stribeutes* sp., *Cacotropa* sp., and *Neleothymus* sp. from low wet tundra; *Mesoleptus* sp. and *Cymodusa* sp. from the bush; *Phobetes* sp. from emergent vegetation of pools; *Phygadeuon* sp. near *liogaster* (Thoms) was parasitic upon *Cynomya cadaverina* larvae working in the skull of a dead husky dog. They emerged from the fly puparia during a four-day period.

Proctotrupoidea:

Platygaster near *confusa* Fouts, and *Platygaster* sp. from tundra flowers; *Isocybus canadensis* Prov.,

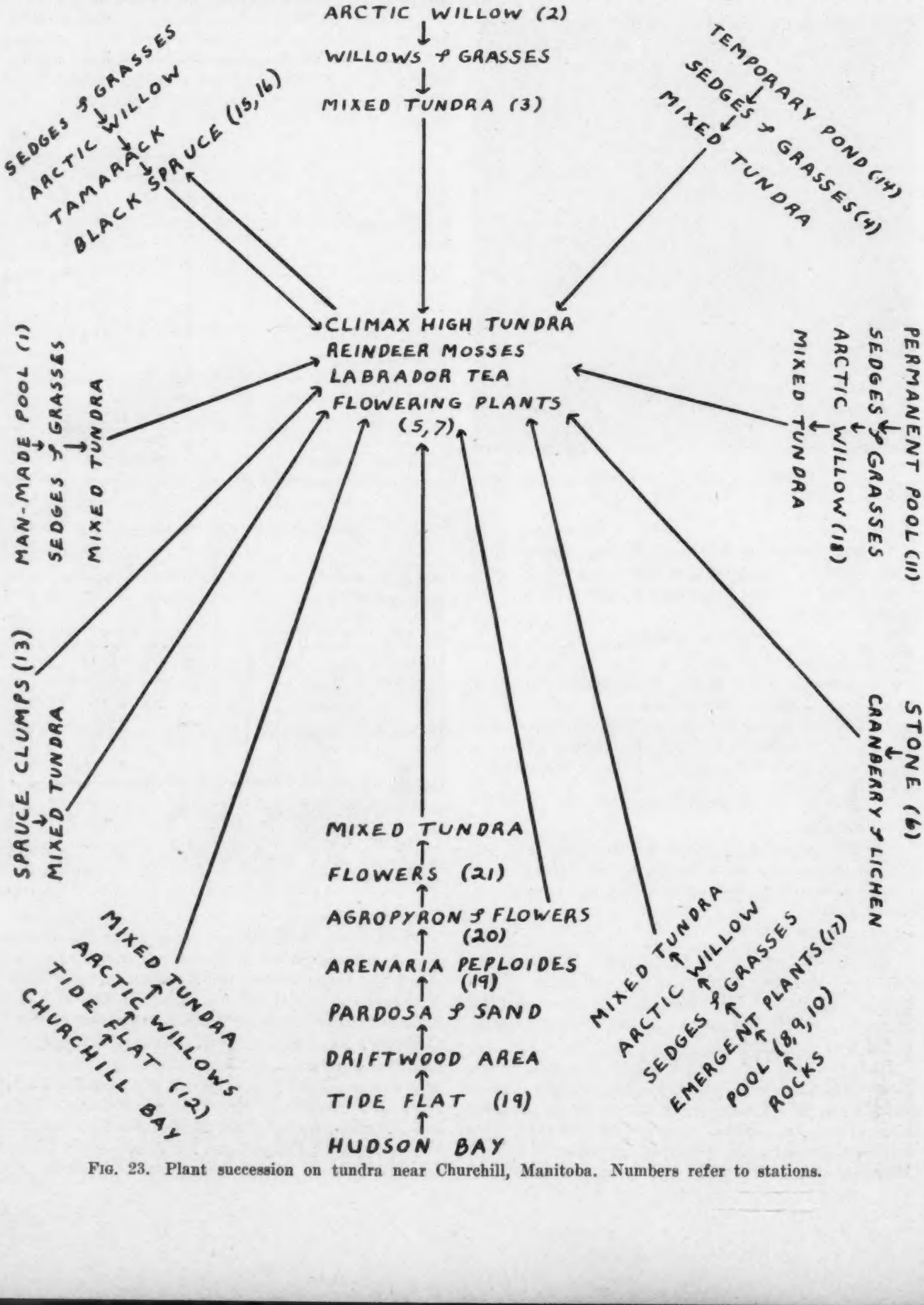

FIG. 23. Plant succession on tundra near Churchill, Manitoba. Numbers refer to stations.

Zelotypa flavipes Ashm., and *Metaclisis* sp. from dwarf willows; *Prosacantha* sp. from isolated spruce clumps; and *Polypeza* sp. from the river tide flats.

Chalcidoidea:

Hypopteromalus sp., *Pteromalus* sp., *Xanthesoma* sp., *Callimomus* sp., *Pleurotropis* sp., *Trigonogastra* sp., *Necremnus* sp., *Terobia* sp. near *vulgaris* Ashm., *Habrocytus* sp., *Harmolita* sp., and *Copidosoma* sp. from tundra flowers; *Sympiesis* sp., *Eurytoma* sp., *Tetrastichus* sp., and *Horismenus* sp. from the river tide flats; *Polycystus* sp., *Bubekia* sp., *Paphagus* sp., and *Syntasis* sp. from isolated spruce clumps; *Gyrolasia* sp. from emergent vegetation of pools; *Hyssopus* sp. from the bush; *Cirrospilus* sp. from dwarf willows; and *Diaulinus* sp. and *Aprostocetus* sp. from low wet tundra.

Formicidae:

But few ants were seen on the tundra, and none were seen in the bush except wood-inhabiting forms. Three species were evident of which the large *Camponotus maculatus vicinus* var. *plurabilis* Walker was only occasionally taken. Colonies of *Formica fusca* var. *gelida* Wheeler and *Myrmica brevinodis* var. *sulcinodoides* Emery were found in a ratio of 12 percent to 88 percent. On June 20, when the bush was deeply flooded from melting snows, ant colonies were found under the loose bark of black spruce stumps. No eggs were evident, and the workers were tending numerous larvae. There was a colony to almost every stump. By June 26, the larvae appeared to be half grown. By July 10, water had drained from the forest so that the ants could retreat to the soil. Following heavy rains, they were back in the stumps with full-grown larvae on July 27. During the next week all larvae pupated and worker pupae made up 72 percent, while winged pupae were 28 percent of the total. Adults probably emerged early in August. On July 1, the only ants seen on the tundra, apparently *Formica fusca,* were on a tundra hummock capturing chironomid adults as quickly as they alighted. The colony was not found.

Sphecidae:

Pemphredon near *foxii* Rohwer found in bush.

Bombidae:

Bumblebees were conspicuous over the tundra. Early in June large lone queens flew about in search of nesting quarters. By the first of July small workers were in the field and were present during the remaining observations. Three species, not closely associated with any habitats, were in numerical ratio as follows: *Bombus sylvicola* Kirby 50 percent; *B. frigidus* F. Smith 30 percent; and *B. balteatus* Dahlbom 20 percent.

POPULATION TREND

As previously stated, arthropod populations were estimated by the sweeping method, 50 sweeps through plants being taken at each collection at each terrestrial station. The average number of insects taken in 50 sweeps during the first week of observation, ending June 14, was six. The average number of specimens during the week of greatest insect activity, ending July 12, was 573. Using the average number of insects collected in 50 sweeps during the first week as 1, it was found that the average weekly collection for the remaining seven weeks fell in direct ratio with this. Figure 24 shows the season's insect activity. Between June 10 and July 5 there was a steady gradual rise in insect abundance and activity.

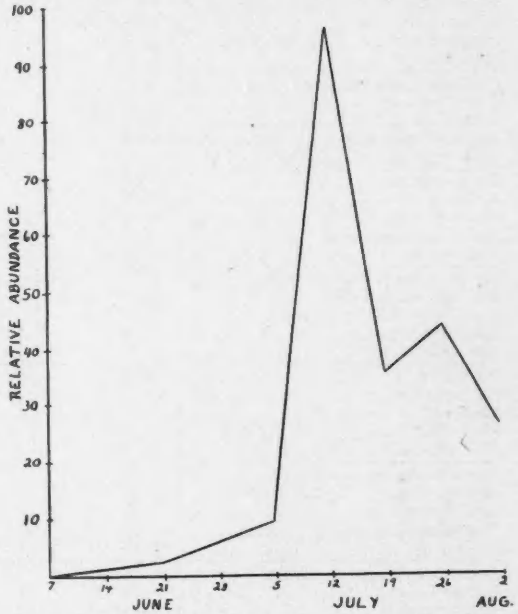

FIG. 24. Showing trend of arthropod populations during the summer of 1936 at Churchill, Manitoba.

During the week of July 12 abundance increased ninefold, being the highest peak of activity of the summer. This was followed by a rapid decline, indicating that the season of high activity was almost over by the first of August. Whether another high peak of activity would occur during August was not determined, but seemed unlikely, because frost occurred soon during that month. Arthropod seasonal activity this far north is reduced to one great peak, whereas 20° farther south there are two great peaks of activity, one in June and one in September.

ASPECTION IN THE VARIOUS TUNDRA TERRESTRIAL HABITATS

STATION 2—DWARF ARCTIC WILLOW ASSOCIES

June 11—Sedges sprouting and willows in flower.

June 22—Willow leaves opening.

June 29—*Petasites* in bloom, willow leaves one-half open.

July 6—Willows in full leaf, *Pedicularis lapponicum* in bloom among willows.

July 13—Willow pods bursting.

TABLE 6. Species of arthropods collected at dwarf arctic willow stations 2 and 18. L, larva; Y, young; A, adult; N, nymph.

Species	From Station	Week of 6/11	6/15	6/22	6/29	7/6	7/13	7/20	7/27
Psyllia fibulata	2	4	8	3					
Tetragnatha extensa	2-18	1Y	0	2Y	2Y	1Y		2Y	2Y
Dasyneura sp.	2		1						
Thrips near *madroni*	2-18		14A	37A	23A	5A	10N	56N	12A&N
Taeniothrips vulgatissimus	2-18		1	1					
Erigone dentigera	2		1	1					1
Eulaira tigana	2		1						
Microneta sp.	2		2Y	1Y					
Clubiona sp.	2-18		1Y	2Y	3Y		1Y	1Y	
Campoplegini	2		1						
Strogylocephalus agrestis	2		1A						
Trioza varians	2-18			4					
Platygaster sp.	2-18			1		2			
Araneus patagiatus	2-18			17Y	20Y	4Y1A	15Y	3Y	9Y
Phidippus sp.	2			1Y					
Dorytomus sp.	18			1L 1A	3A				
Aedes sp.	2-18				6		122	25	11
Pteromalus sp.	2-18				1	1	1		
Sericus incongruus	18					1			
Podabrus sp.	2-18					2	1	2	
Melanostoma near *chaetopoda*	2					1			
Phyllodecta americana	2					1L	1L		
Aedes nearcticus	2-18					259			
Simulium vittatum	2-18					2080	2		1
Monoblastus sp.	2					1			
Pimpla sp.	2					1			
Zootrephes sp.	2					1			
Tenthredinid larvae	2-18					3L5A	17L	8L2A	10L
Micryphantidae	2-18					2Y			8Y
Psyllia breviata	2-18					1	6	9	7
Baetis brunneicolor	18					1		4	
Pentapleura sp.	18					1			
Zaplethecornia sp.	18					1			
Phaeogenes gaspesianus	18					1			
Aclastus sp.	18					1			
Prionocera sp.	18					1			
Cirrospilus sp.	18					1			
Microbracon sp.	18					1			
Adela sp.	18					2			
Epistrophe sodalis	18						1		
Aphis sp.	18						1		
Ichneutes sp.	18						1		
Epiurus near *bicoloripes*	2-18						1		1
Anaphothrips sp.	2-18						26		
Mesocrina sp.	18						1		
Simulium venustum	2-18						1	4	18
Tipula sp.	2						2		
Limonia sp.	2						1		
Campoplex sp.	2						1	2	1
Euphorus pallipes	2						1		
Tabanus illotus	2-18							2	1
Tabanus affinis	2							1	
Apanteles sp.	2							1	
Hemimachus sp.	2							1	
Aphidius sp.	2							1	
Alysia sp.	2							1	
Teratocoris herbaticus	2							2	
Salticidae	2							1Y	
Terobia near *vulgaris*	18							1	
Callidiotes sp.	18							3	
Mesoleptini	18							1	
Proterops sp.	18							1	
Gelis sp.	18								1
Meteorus dimidiatus	2								1
Trichoptera	2-18					3	1	1	1
Plecoptera	2-18						1		1
Acarina	2-18				1	4			
Chironomidae	2-18			7	131	1299	309	2019	219
Diptera	2-18		1	2	29	112	53	86	8
Mycetophilid	2				3	8	1	2	
Total		5	32	81	222	3809	580	2242	313

TABLE 7. Soil fauna from one square foot samples of tundra mat. Y, young; L, larva; P, pupa; N, nymph.

Species	Found in Station	Week of								
		6/12	6/16	6/24	6/30	7/7	7/14	7/21	7/28	Total
Dyschirius sp.	3	1		1			1	1		4
Folsomia elongata	2-3-5-7	19		89	2	10	1	1		122
Isotoma olivacea	3-5-7	1	3	3	3	3	4	12	2	31
Isotomurus palustris	2-3	7					17			24
Hymenoptera	3	2								2
Acarina	2-3-5-7	54	137	288	259	181	172	240	171	1502
Isotoma sp.	2-3-5	2	4		1				15Y	22
Isotoma viridis	2-3-5-7	1	6	2	6	50	47	19	13	134
Entomobrya nivalis	5-7	2	2	11	13	3	6	4	4	45
Trichocellus porsildi	3-7	2		2	2	1				7
Staphylinidae	3		2							2
Folsomia fimetaria	2-3-5-7		1	1	1	2	1		1	7
Micryphantidae	2-3-5-7		2Y	1Y	1Y	12Y	13Y	29Y	11Y	69
Micranurida pygmaea	2-3-7		1		1			4		6
Folsomia diplophthalma	3-5		2						1	3
Diptera larvae	2-3-5-7		2	6	2	5	25	20	26	86
Folsomia quadrioculata	2-3-5-7			3	1	7		1	4	16
Isotoma bipunctata	2-3-5-7			3	6	4	4	7	1	25
Argenna sp.	7			1Y						1
Noctuidae	3-7			1L				1L	1L	3
Lycosa sp.	2-7				2Y		1			3
Entomobrya near *muscorum*	3-5				1					1
Anurophorus laricis	3-5				7	3		1		11
Onychiurus sp.	2-3				2	3Y			2Y	7
Ilybius angustior	2				1L					1
Friesea mirabilis	2-3-7					1	2	3	3	9
Onychiurus groenlandicus	2					2				2
Sminthurides pumilis	2					1	8	1	1	11
Arrhopolites sp.	2-5-7					2	4	3	1	10
Tabanus sp.	5					1L				1
Pardosa sp.	3-7					1Y	1Y			2
Achorutes armatus	3-5-7					2			3	5
Harpalini	7					1L				1
Clubiona sp.	7					1Y				1
Melanophthalma americana	2						1			1
Tetracanthella sp.	7						1			1
Oxyptila sp.	2-3						2Y	1Y		3
Cantharis mandibularis	7						1L	1L		2
Grammonota sp.	2						1Y	8Y		9
Podabrus sp.	3						1L			1
Nysius sp.	3						1N	1N		2
Chamydatus pullus	2-5						2N			2
Macrosteles fasifrons	2						2N			2
Vertigo ventricosa	2						1			1
Sminthurides occultus	2							1	1	2
Terebrantia	2							1P	1P	2
Eularia tigana	2							5		5
Montilaira sp.	2							1		1
Microneta sp.	2							1		1
Cornicularia sp.	2							1		1
Tortricidae	2							1L		1
Diplosid sp.	3							1		1
Grammonota inornata	5								1	1
Frankliniella tritici	3-5								2	2
Aphis sp.	3								1	1
Arpedium sp.	2								2	2
Succinea grosvenori	2								4	4
Total		91	162	412	311	296	323	367	272	2234

July 20—Willows throwing cotton, *Habenaria* and *Castilleja* in bloom.

July 27—*Castilleja* in full bloom, *Petasites* throwing seed.

Station 2 was distinctive in that it supported one of the highest number of arthropod species. Since this type of habitat was widely distributed over the tundra, and since many isolated willows occurred at different habitats, it did not have a group of indigenous fauna. The *Thrips* near *madroni,* although found throughout the tundra, was the most abundant here. During June adults were found; during July the population was mainly nymphs. A new generation of adults appeared the first of August. The spider, *Araneus patagiatus,* occurred throughout the tundra, but was most abundant in these willow habitats. Young were found throughout the summer and adults late in the season. Probably because of the large amount of leaf surface available for resting purposes, black flies reached their greatest abundance here. During the week of July 6 as many as 2,000 were taken in 50 sweeps of the net. Willow leaves were eaten by the larvae of the flea beetle, *Phyllodecta americana,* and the moth, *Hillia iris,* Numerous tenthredinid larvae also fed extensively throughout the willow habitats. Table 6 lists the species and number of arthropods taken in this habitat. Examination of this and the following tables concerning the different habitats will show the succession of organisms as they appeared from week to week.

One square foot soil samples to the depth of one inch were taken at this station and at Stations 3, 5, and 7. During the first three weeks of observation Station 2 was inundated so that no soil samples could be taken. The conspicuous thing concerning soil debris inhabitants was their uniformity throughout the tundra. Except for minor variations, the species of Collembola were the same at all habitats. At Station 2 *Isotoma viridis* apparently reached its greatest abundance. This was also the case with *Sminthurides pumilis.* More than 33 species of arthropods were found inhabiting the soil and these are listed in Table 7.

Station 3—Mixed Tundra

June 11—Mixed tundra with hummocks of reindeer mosses and patches of sedges and willows between them.

June 15—Willow leaf buds opening.

June 22—Willow in full flower, cranberry in bloom, other plants growing.

June 29—*Rhododendron lapponicum, Petasites sagittatus, Draba arabisans, Androsace diffusa, Saxifraga tricuspidata, Ribes setosus, Rubus chamaemorus* in bloom; *Achillea millefolium* sprouting.

July 6—*Eriophorum capitatum, Dryas integrifolia, Pedicularis lapponicum, Pedicularis* sp., *Astragalus* sp., *Rhododendron lapponicum, Andromeda* sp., *Saxifraga tricuspidata, Stellaris* sp., and *Pedicularis groenlandica* in bloom. *Pyrola uliginosa* and *Epilobium lineare* in bud.

July 13—*Astragalus crassicarpus* in full bloom. *Eriophorum capitatum* and *E. vaginatum* in fruit and throwing cotton. *Dryas integrifolia* fruit green. *Caltha palustris* in bloom. Most of the other flowers past bloom.

July 20—*Astragalus* still in bloom. *Eriophorum* spp. throwing seeds and most flowers in fruit.

July 27—*Petasites, Draba incana, Astragalus, Eriophorum,* and *Dryas* in seed. *Epilobium angustifolium* and *Castilleja* in full bloom.

The mixed tundra (Fig. 5), because of its nature, had representatives of fauna from all of the other habitats about it. Few, if any, of the insects collected there were indigenous or could serve to identify this type of habitat. No particular forms except black flies were ever in great abundance. Table 8 lists the species taken and indicates their succession of appearance during the season. A much smaller group of species is represented here than in the previous habitat. This again is probably due to the mixed nature of the plants present.

The soil fauna of Station 3 agreed in species with that of the tundra habitats. Here the small carabid *Dyschirius* sp. was present among the lichens, and also *Trichocellus porsildi* were common. Collembola, *Folsomia elongata,* was the most abundant in this habitat. Another Collembola, *Anurophorus laricis,* appeared here as well as at Station 5. Table 7 lists the soil fauna of some 30 species for this station.

Station 4—Low Tundra *Eriophorum* Associes

June 11—Full stand of sedges, mainly *E. capitatum* and *E. vaginatum.* All plants stiff and dry. Station inundated.

June 22—New plants sprouting.

July 6—Sedges blooming, also *Ranunculus* in bloom. Station flooded again from rains.

July 13—Sedges in full bloom.

July 27—Sedges throwing seeds (Fig. 4).

Although this habitat had the smallest variety of plants, it had the greatest number of species of insects active over it. Most conspicuous of these was the number and variety of parasitic Hymenoptera. Collembola clung to the stems of sedges and at any disturbance leaped into the water. During the first week of observation the Collembolan population averaged three per square foot of water surface. In the next week or so this dropped to one. Staphylinids of the genus Stenus were typical of this habitat. The tipulids *Prionocera* sp. and *Limnophila mcclureana* were most abundant in this associes. Table 9 lists the fauna of the *Eriophorum* associes.

TABLE 8. Fauna collected from plants of mixed tundra—Station 3. A, adult; L, larva; N, nymph; Y, young.

Species	Week of 6/11	6/15	6/22	6/29	7/6	7/13	7/20	7/27
Microbracon gelechiae		1						
Habrocytus sp.		1						
Thrips near *madroni*			1	3A&N	2A&N	1	12A&N	
Spiropalpus spiralis			1					
Micryphantidae			2Y		1Y			
Tortricidae			1L					
Entombrya nivalis				1				
Melanoplus borealis borealis				1N				
Aedes sp.				3		43	1	1
Orgilus sp.				1				
Melanostoma pictipes					1			
Aedes nearcticus					5			
Psyllia breviata					4	12	9	1
Phygadeuon sp.					1			
Simulium vittatum					484			
Aptinothrips rufus					1			
Prionocera sp.					1			
Stenus occidentalis					1			
Tenthredinidae					2Y		1	
Tabanus illotus						1		
Terobia near *vulgaris*						1		
Anaphothrips sp.						1		
Terebrantia						4Y		
Tipula near *sulphurea*						1		
Crambus sp.						1		
Baetis sp.							1	
Deuterosminthurus insignis							5	
Meteorus sp.							1	
Tipula near *appendiculata*							1	
Limnophila near *poetica*							1	
Panimicra sp.							1	
Rhizarcha sp.							1	
Delphacodes sp. near *kilmani*							2A	2 N
Chamydatus pullus							1	
Micryphantidae							2Y	
Macrosteles fascifrons							5A	
Trichoptera					1			
Mites				5				
Chironomidae			1	3	32	14	11	2
Mycetophilid				1			1	
Diptera					16	12	13	8
Total	0	2	6	18	550	91	69	14

STATION 5—CLIMAX HIGH TUNDRA WITH SOUTHERN EXPOSURE

June 12—Dominant plants reindeer mosses, cranberry, prostrate spruce *(Picea mariana)*, and *Chamaecistus procumbens* in localized patches.

June 16—*Saxifraga oppositefolia* in bloom. *Rhododendron lapponicum* in bud. Leaves of *Saxifraga tricuspidata* turning red.

June 24—*Rhododendron* still in bud, old fruit hanging on *Ledum palustre*.

June 30—*Rhododendron* and *Marronia alpina* blooming. Fungus *Calvatia* sp. sprouting.

July 7—*Dryas integrifolia* blooming profusely. *Astragalus* sp. starting to bloom and *Rhododendron* past bloom.

July 14—Dryas past bloom. *Pinquicula vulgaris* and cranberry in bloom.

July 21—Most flowers past bloom.

July 28—*Dryas* in seed. *Saxifraga tricuspidata* still blooming. Almost all other flowers in seed.

TABLE 9. Fauna of the sedge associes—Station 4. A, adult; Y, young; N, nymph.

Species	Week of 6/11	6/15	6/22	6/29	7/6	7/13	7/20	7/27
Erigone dentigera	1							
Tetragnatha extensa	1Y				1A	1Y		
Oedothorax sp.		1						
Campoplex sp.		1						
Staphylinidae		1						
Diptera		1	6	11	10	60	74	33
Araneus patagiatus			2Y			1Y		
Stenus retrusus			1					
Isotumurus palustris				1				
Aedes nearcticus				6	6	77	25	3
Aphis monardae				1				
Microbracon sp.				1				
Apanteles sp.				1		1		
Thrips near *madroni*				2			4A&N	
Clubiona sp.				2Y				
Micryphantidae				5Y	1		7Y	
Habrocytus sp.					1			
Simulium vittatum					90			
Prionocera sp.					5	12	2	
Tipula sp.					1			
Isocybus canadensis					3	1	1	
Teratocoris herbaticus					1N		5A&N	
Tabanus zonalis					1			
Podabrus sp.						1		
Deuterosminthurus insignis						7	32	1
Epiclista sp.						1		
Phygadeuon sp.						1		
Anaphothrips sp.						5		
Limnophila mcclureana						2	1	
Scopesis sp.						1	2	
Zaphleges sp.						1		
Mesoleptini						1		
Neleothymus sp.						1		
Tetrastichus sp.						1		
Chlamydatus pullus						4N		
Laevicephalus striatus						1N	3N	
Coenocara scymnoides							1	
Succinea grosvenori							2	
Simul um venustum							4	1
Limnophila near *poetica*							1	
Delphacodes sp. near *kilmani*							1	
Adelius sp.							1	
Diaulinus sp.							1	
Exolytus sp.							1	1
Pezoporus sp.							1	
Symplesis sp.							1	
Pimpla sp.							1	
Cacotropa sp.							1	
Podura aquatica								1
Dacnusa sp.								1
Aprostocetus sp.								1
Stenomacrus sp.								1
Isomerista sp.								1
Metaclisis sp.								2
Phygadeuonini								
Trichoptera					1	3	2	5
Tenthredinidae					1			
Mites						8		
Chironomidae			2	29	15	22	17	2
Total	2	4	11	59	137	213	191	55

As is usual with most climax communities, the fauna of the high tundra even in its southern exposures was the smallest of all tundra habitats. Most conspicuous of the arthropods was a running spider, *Pardosa* sp., which hunted on the surface of the sphagnum catching any flies which alighted near it. During the first two weeks of July the females of these spiders were dragging egg cocoons. By the end of the month the eggs had hatched. The species taken here included *Entomobrya* near *muscorum*, *Pardosa* sp., *Aedes punctor*, *Prionellus* sp., *Simulium venustum*, *Aedes* sp., *Melanoplus borealis borealis*, *Phaedon oviformis*, *Isocybus canadensis*, and several miscellaneous flies. Mosquitoes were most abundant during the week of July 14, and the greatest number of species was taken during the week of July 21.

Soil fauna was similar to that of the rest of the tundra, 20 species being identified. Of these, the Collembolan, *Entomobrya nivalis*, reached its greatest abundance in this area.

STATION 6—CRANBERRY-LICHEN ASSOCIES

June 16—Rocks with lichen *Parmelia* sp. and cranberry over them. Cranberries shrinking.

June 24—Birds, especially snowbirds and sparrows, have eaten many of the cranberries.

June 30—Most berries gone. Flowers in bud.

July 7—Cranberry buds in the pink.

July 14—Cranberries in bloom.

July 21—Cranberries still in bloom with old berries clinging to plants.

July 28—Plants bear both green and ripe berries.

This type of habitat seemed to have no or almost no indigenous fauna. The cranberries were not noted to be attacked by any insects and none were seen feeding on lichens. The tundra running spider, *Pardosa concinna* (Fig. 20C), appeared here running into the station from surrounding plants.

STATION 7—CLIMAX HIGH TUNDRA

June 12—Much dead reindeer moss, *Usnea*. Reindeer moss growth not as luxuriant as in Station 5. Sphagnum, overlaying rocks and gravel, thinner. Prostrate willows, prostrate spruce, cranberry, and Labrador tea distributed over area.

June 24—Flowering plants growing, but no flowers.

June 30—*Rhododendron lapponicum* in bloom, other plants in bud.

July 7—*Ledum palustre, Dryas integrifolia, Rhododendron, Ribes hudsonicus, Rubus chamaemorus, Habenaria, Ranunculus, Astragalus, Cerastium alpina, Primula egaliksensis, Loiseleria procumbens, Vaccinum,* and *Saxifraga caespitosa* in bloom. *Pyrola uliginosa* in bud.

July 14—*Ledum, Habenaria obtusata, Habenaria* sp., *Polygonum viviparum* in bloom. *Astragalus* past bloom, willows throwing seed. *Epilobium angustifolium* in bud.

July 21—Most plants past bloom.

July 28—*Dryas* in seed. *Rubus* berries ripening.

The high climax tundra (Fig. 9) was more sparse and less luxuriant than at Station 5 because of exposure to extreme winds and low temperatures. Its fauna was as scarce as that of Station 5 and here, too, the Pardosa was the most conspicuous animal. Five more species were taken here and the list included *Psyllia fibulata, Entomobrya nivalis, Pardosa* sp., *Aedes* sp., *Podabrus* sp., *Aedes nearcticus, Simulium vittatum, Delphacodes albostriata, Cantharis mandibularis, Tabanus illotus, Araneus* sp., *Aphis* sp., and several Diptera. Greatest number of species and individuals was taken during the week of July 7. The soil fauna (Table 7) of high tundra does not show much variation from that of the rest of the tundra. Mites were especially abundant here. As in Station 5, the Collembolan *Entromobrya nivalis* was abundant. Larvae of the beetle *Trichocellus porsildi* and *Cantharis* sp. were found among the lichens probably feeding on Collembola and other small insects.

STATION 12—CHURCHILL BAY TIDE FLATS

June 20—Ice piled over tide flat.

July 3—Tide flat clear of ice, and grasses have grown up.

July 17—Grasses in head. *Ranunculus* and *Primula egaliksensis* in bloom.

July 24—Grasses in fruit.

July 31—*Parnassia palustre, Chrysanthemum* and *Ranunculus* in bloom.

The fauna of this area was extensive, including over 50 species. The two most conspicuous organisms were the carabid, *Dyschirius nigripes*, and the saldid, *Salda littoralis*. This area was inundated regularly from tides (Fig. 6) which raised the water in Churchill Bay, but not to a depth which exceeded the height of the grass. By the first of July it was free of ice, and, when not covered with water, the Salda nymphs running over the ground averaged ten per square foot. Dyschirius averaged three per square foot. At this time, temporary pools at the edge of the tide area were alive with mosquito larvae and pupae which numbered about 200 per square foot of water surface. By July 24 Salda nymphs were fullgrown and adults were present, and by this time they had increased to about 25 per square foot. Two species of fulgorids of the genus Delphacodes were taken only in this area and were abundant here. Three species of leaf hoppers of the genus Macrosteles were also abundant. They were all in nymphal condition until the last week of July, when adults began to appear. The eighth indigenous insect was the small anthocorid, *Teratocoris herbaticus*, which appeared regularly in the sweepings. These eight insects, restricted to this habitat, gave it definite character. Table 10 lists the insects taken here.

TABLE 10. Species of arthropods taken at Churchill Bay Tidal Flats—Station 12. N, nymph; Y, young; A, adult.

Species	Week of				
	7/3	7/10	7/17	7/24	7/31
Dyschirius nigripes	4				
Aedes sp.	4	38	4		15
Pericoma sp.	1				
Simulium vittatum	88	50			6
Anaphothrips sp.	27	12	89	42	
Prionocera sp.	1				
Nysius sp.	11N				
Delphacodes sp. near *kilmani*	1N	34A	10		1N 1A
Macrosteles fascifrons	4N	132N	130N	41A 29N	3N 339A
Chirothrips manicatus		5	4	3	1
Aptinothrips rufus		6			
Thrips near *madroni*		9			4
Erioptera sp.		1			
Araneus sp.		2Y	1Y	3Y	
Phygadueonini		1			
Sympiesis sp.		1			
Eurytoma sp.		1			
Platygaster sp.		2			
Delphacodes pellucida		3A	23A	8N	
Teratocoris herbaticus		1N	2N	6A	18A
Collembola		1			
Aphis sp.			2	1	
Syrphoctonus minimus			1		
Frankliniella tritici				1	
Tetragnatha sp.				1Y	
Homelys sp.				1	
Chorebus sp.				1	
Salda littoralis				1N 25A	
Laevicephalus striatus				7N	
Macrosteles divisus				102A	5N 21A
Macrosteles near *sexnotatus*				19A	19A
Monardia sp.					1
Simulium venustum					11
Zilla sp.					3Y
Micryphantidae					2Y
Habromma sp.					1
Bathymetis sp.					3
Cryptinae					1
Tryphoninae					3
Tetrastichus sp.					7
Horismenus sp.					1
Polypeza sp.					2
Melanotrichus sp.					1
Laevicephalus asper					1A
Chlamydatus pullus					1A
Trichoptera				1	3
Tenthredinidae		2			1
Staphylinidae					1
Chironomidae	17	127	42	35	119
Diptera	7	90	56	91	81
Total	165	518	364	418	676

STATION 13—ISOLATED BLACK SPRUCE CLUMPS

June 14—Snowbanks piled among and around trees.

June 20—Snow gone, tips of leaves green.

July 3—Cones beginning to form.

July 10—Spruce covered with cones which were shedding their scales.

July 24—New twig growth about an inch and a half long. Cones continuing to grow.

July 30—Cones over an inch long.

This was another highly characteristic localized habitat of the tundra (Fig. 8). It was identified by abundant spiders, especially the species *Araneus patagiatus* and *Pityohyphantes limitanea.* They spun webs so that trees were almost encased and fed upon numerous flies which became entangled. Since the small trees rising into the air above the level tundra would feel the full force of the wind, spiders had an ideal place for their nets. Early in the season, chermids of at least three species were abundant on the spruce and probably fed upon it. Table 11 lists the species found here.

TABLE 11. Animals inhabiting isolated clumps of black spruce—Station 13. Y, young; A, adults.

Species	Week of							
	6/14	6/20	6/26	7/3	7/10	7/17	7/24	7/31
Entomobrya near *muscorum*	1							
Aphalara nigra	13	20				1N		
Pardosa sp.	1Y							
Psyllia brevistata		1						
Psyllia fibulata		2	2	2				
Tetragnatha sp.		1Y						
Paphagus sp.		1						
Pteromalus sp.		1					1	
Araneus patagiatus			3Y	4Y	2Y	5Y	1Y	3Y
Pityohyphantes limitanea			2Y	1Y	6Y	1Y	4A	1Y
Ebo pepinensis			1					
Polycystus sp.			1					
Aedes nearcticus				19	72	14	8	4
Simulium vittatum				1	22			1
Monoblastus sp.				1				
Meteorus vulgaris					1			
Dinotrema sp.					1			
Habrocytus sp.					2			
Bubekia sp.					1			
Trichoptera					1			
Diptera					1			
Tabanus affinis						1		
Terobia sp.						1		
Simulium venustum						2		4
Simulium corbis						1		
Chrysops furcata						3		
Delphacodes near *kilmani*						1		
Prosacantha sp.						1		
Syntasis sp.						2		
Mesoleptini						1		
Dictyna volucripes							4	1
Dictyna vincens							1	
Tenthredinidae							1	2
Tryphoninae							1	
Habrocytus sp.								1
Chironomidae	3	2	4	8	78	8	7	12
Diptera	1	5	10	1	23	15	18	17
Total	19	33	23	37	210	57	46	46

STATIONS 15 AND 16—THE BLACK SPRUCE-TAMARACK FOREST OR BUSH

June 11—Area flooded with water from melting snow. Snowbanks four or five feet deep.

June 20—Tamarack buds opening, spruce tips greener, willow in bud.

June 26—Tamarack, willow, and herb leaves opening. Snow gone except in patches. Grasses, sedges, *Equisetum, Epilobium,* and *Lesquerella* sprouting.

July 3—Willows and tamarack in full leaf. Still some snow drifts, but most of water drained away.

July 10—Tamarack cones forming. *Habenaria, Ledum, Verbena, Rubus arcticus, Caltha palustris,* and *Castilleja* in bloom.

July 17—Willows in fruit, *Eriophorum* and *Poa triflora* heading. Labrador tea and orchids in bloom.

July 24—Tamarack cones larger, shelf fungus *(Lenzites saepiara)* growing on spruce logs. Grass three or four feet tall.

July 31—Some willow leaves yellowing. *Parnassia palustre, Habenaria* and *Epilobium angustifolium* in bloom. *Rubus* berries ripe.

Although the spruce-tamarack forest, or bush as it is referred to, is not part of the tundra proper, it cannot be ignored in this area because of the interchange of plants and animals between it and the tundra (Fig. 16). Even though it is very sparse, the trees do not reach great height, and it is impregnated with reindeer mosses and tundra plants; it seems like a jungle after working on the tundra. Only two distinct layer societies were represented, that of the trees and that of the herbs and shrubs. Tree fauna was smaller than at lower levels, but bore a great similarity to that of isolated spruce clumps. Spiders were again the most consistently abundant forms. *Araneus patagiatus* was represented here, but another *Pityohyphantes* species took the place of that of isolated clumps. In addition, there were several other species of spiders. Chermids were abundant in the tree layer as they were in the isolated clumps.

Fauna of the herb and shrub layer was extensive including over 50 species. The spider *Tetragnatha extensa* was most abundant in the bush, appearing only occasionally on the tundra. The bush was characterized by three distinct forms—grasshoppers, dragonflies (Fig. 18A), and horseflies. The six species of dragonflies were in ratio of abundance as follows: *Aeshna juncea americana,* 43 percent; *A. sitchensis,* 18 percent; *A. coerulea septentrionalis,* 10 percent; *A. eremita,* 5 percent; *Somatochlora albicincta,* 18 percent; and *S. whitehousei,* 5 percent. Both Tabanus and Chrysops were plentiful. Nymphs of grasshoppers, *Melanoplus borealis borealis,* began hatching the last of June and became adult by the last week of July. They were most numerous along the railroad right-of-way and on hummocks within the bush. Probably the eggs were laid in these situations since all lower areas were inundated for a period long enough to drown the eggs. Tables 12 and 13 list the arthropods taken.

TABLE 12. Arthropods of tree layer society of black spruce-tamarack forest—Station 15. L, larva; Y, young; A, adult.

Species	WEEK OF							
	6/11	6/20	6/26	7/3	7/10	7/17	7/24	7/31
Trioza varians	1							1
Aphalara nigra	1	2						
Tetragnatha extensa	2Y		2Y			1A	4Y	1A
Pityohyphantes phrygiana	3Y	1Y	3Y	1A	1A	2Y	3Y	
Dictyna sp.	1Y	1Y					2	
Diptera	1		2	5	7	6	2	
Cyphon variabilis		1						
Psyllia fibulata		1						
Philodromus sp.		1Y		1Y		1Y	1Y	
Araneus patagiatus		1Y		3A	2Y	1Y		
Aphis sp.			3					
Helobia hybrida			1					
Zilla sp.			1Y					
Hypselistes florens			1					
Dictyna sublata			1					
Aedes sp.				37	30	31	8	14
Noctuid				1				
Tabanus rhombicus					1	2		
Tabanus affinis					1	2	2	
Simulium vittatum					11			
Simulium venustum					2	20	15	34
Terobia sp.					1		1	1
Dictyna muraria					1			
Limnophila near *platyphallus*						1		
Chrysops furcata						1	1	
Syntasis sp.						1		
T· nthredinid						1L		
Laevicephalus striatus							1	
Psyllia breviata								1
Mesoleptus sp.								1
Cymodusa sp.								1
Chironomidae			6	3	27	8	3	
Total	9	8	20	51	85	78	43	54

STATION 17—EMERGENT VEGETATION IN PERMANENT POOL

Pool Station 17 had the only extensive emergent vegetation area (Fig. 12). These plants were swept at each observation and bore a representative fauna made up mainly of the adults of aquatic insects. Chironomids were the most numerous forms, for over 1500 were taken on July 6 and 700 on July 13. The damsel fly, *Coenagrion resolutum,* bred in this pool and adults rested upon the vegetation. They began emerging during the first week of July, reached their peak during the week of July 13, and were gone by July 25. Nymphs that were collected during June emerged at the same time as those in the wild. *Prionocera* sp., noted in Station 4, was also represented

TABLE 13. Arthropods taken in herb and shrub layer society of black spruce-tamarack forest—Station 16. L, larva; N, nymph; Y, young; A, adult.

Species	Week of							
	6/11	6/20	6/26	7/3	7/10	7/17	7/24	7/31
Entomobrya near *muscorum*	1		1					1
Psyllia fibulata	3							
Tetragnatha extensa	3Y		3Y			2A	4Y	3Y
Microneta sp.	2Y							
Delphacodes albostriatus	2							
Trioza varians		3						
Micryphantidae			1Y	2Y		1Y	1Y	
Phyllodecta americana				1	2	1		
Aedes nearcticus				28				
Aedes punctor				19				
Araneus patagiatus				2Y	2A	2A		
Dictyna sp.				1				
Autographa sp.				1L				
Argiopidae				1Y				
Tabanus rhombicus					1			
Aedes sp.					68	39	12	12
Aspilota sp.					1			
Simulium vittatum					6			
Thrips near *madroni*					1N 1A	1 N	2N 1A	
Prionocera sp.					1			
Adialytus sp.					1			
Delphacodes sp. near *kilmani*					1			
Mites					5		25	
Melanoplus borealis borealis						1		
Simulium venustum						34	6	13
Chrysops furcata						1		
Pityohyphantes phrygiana						1	1	
Bathyphantes sp.						1Y		
Compoplegini						1		
Zelotypa floripes						1		
Hyssopus sp.						1		
Trichoptera						2		
Tabanus affinis							2	
Oedothorax sp.							1	
Psyllis breviata								2
Dictyna sublata								1
Homelys sp.								1
Zootrephes sp.								1
Dictyna muraria								1
Macrosteles sp.								1
Tenthredinidae					3L	2L	1L	3L
Chironomidae				9	32	54	3	9
Diptera		2		1	4	7	2	4
Total	11	5	5	65	129	152	61	52

here. Trichoptera were numerous, and the anthocorid, *Teratocoris herbaticus,* was also found here. The 20 species, excluding Chironomidae, Trichoptera, and miscellaneous Diptera, representing this habitat were: *Lathridius cinnamopterus, Nysius* sp., *Aedes nearcticus, Prionocera* sp., *Phalacrocerca* near *neoxena, Coenagrion resolutum, Chlamydatus pullus, Tabanus affinis, Thrips* near *madroni, Chirothrips manicatus, Chrysops furcata, Gausocentrus* sp., *Aclastus* sp., *Gyrolasia* sp., *Tetrastichus* sp., *Aphanta* sp., *Zootrephes compressiventris, Teratocoris herbaticus, Tetragnatha extensa,* and *Phobetes* sp. The weeks of July 6 and July 13 were those of greatest insect activity.

STATION 18—WILLOWS BORDERING LAKE ANNABELLE

June 25—Willows in bloom.

July 1—Willows in full bloom and half leaf.

July 8—Willows in full leaf and fruit green.

July 15—Willow buds bursting and throwing seed. *Anemone richardsonii* blooming among willows.

July 22—Willows in full cotton.

July 29—Most seed gone from willows.

The fauna of willow habitats did not vary much, but in situations as this (Fig. 13) it reflected the presence of aquatic forms of the lake. *Thrips* near *madroni* and *Araneus patagiatus* were abundant here and so were chermids. Adults of Pleocoptera, Ephemerida, and Trichoptera rested on these plants after emerging from the lake. Chironomid population on these was also much higher than willows out on the tundra and since the chironomid flight came the week of July 22 this was the period of greatest activity in this station. Table 6 lists the species taken.

STATION 19—*Arenaria* ASSOCIES

July 2—*Arenaria peploides* forming dense mats on sand (Fig. 10).

July 11—*Arenaria* in full bloom.

July 16—*Arenaria* one-half bloom, one-half green fruit.

July 23—Blooms gone.

July 31—Fruit ripening.

The characteristic arthropod of this sand area was the running spider, *Pardosa groenlandica.* The total fauna was restricted and only occasional insects were taken hovering above the mats of *Arenaria. Pardosa* hunted over the sand and hid under the plants. Other species included *Aedes nearcticus, Simulium venustum, Laevicephalus striatus, Chlamydatus pullus, Simulium vittatum, Elater* sp., and *Bracon solidaginis.* Insects were most numerous during the week of July 11.

STATION 20—*Agropyron-Draba* ASSOCIES

July 2—A mixture of grasses and flowering plants. Grass eight inches high. *Agropyron dasystachium* dominant; *Androsace diffusa* and *Draba incana* subdominant. *Saxifraga tricuspidata, Ranunculus purshii, Astragalus crassicarpus, Cerastium alpinum, Potentilla nivea,* and *Dryas integrifolia* in bloom. *Achillea lanulosa* not in bloom.

July 11—*Astragalus, Taraxacum, Saxifraga tricuspidata,* and *Mertensia lanceolata* in bloom.

July 16—*Astragalus, Taraxacum, Achillea,* and *Chamaenerion latifolium* in full bloom. Rest of flowers past bloom. *Agropyron* heading.

July 23—*Chrysanthemum arcticus, Astragalus, Achillea, Castilleja, Taraxacum, Saxifraga tricuspidata* still in bloom. Fungus puffball, *Calvatia cretacea,* in fruit.

July 30—All flowers in seed or past bloom except *Achillea, Epilobium angustifolium* and *Lappula texana. Agropyron* ripening.

Because of abundant flowering plants (Fig. 11), this habitat had a very extensive fauna. Several species were characteristic here. Among these were the leaf hoppers, *Laevicephalus striatus.* They were in a nymphal condition during June, but adults began to appear the first part of July. By August 1 nearly all had become adults. Much less numerous was the fulgorid *Delphacodes campestris.* They reached maturity during the latter part of July also. Among the flowers, probably searching for pollen, was the small proctotrupid *Platygaster confusa.* During July they were very abundant. Two of the thrips, *Aeolothrips fasciatus* and *Thrips tabaci,* were most numerous here. The true European form of the tarnished plant bug, *Lygus pratensis,* was found among these flowers. Another Hymenopteran, *Pteromalus* sp., although widely distributed over the tundra, was most abundant here. Table 14 lists the species taken.

STATION 21—CERASTIUM-DRABA ASSOCIES

July 2—All of the flowers of Station 20 in bloom.

July 11—*Draba arabisans, Taraxacum erythroperum, Mertensia lanceolata,* and *Cerastium alpinum* in bloom.

July 16—Most of the flowers past bloom or in fruit. *Achillea millefolium* in bloom.

July 23—*Epilobium* and *Castilleja* in full bloom. *Dryas, Cerastium* and *Draba* in seed. *Achillea* and *Saxifraga tricuspidata* still in bloom. Rest of flowers in seed.

This station was similar to Station 20 except that the grasses were absent and reindeer mosses were becoming dominant. Its fauna was therefore not greatly different from the previous station. The mirid, *Chlamydatus pullus,* was most abundant. It was represented by nymphs during June, but they all became adults during July. Another mirid representative of this area was *Nysius* sp. It did not become adult until almost the end of July. The leaf hopper, *Laevicephalus striatus,* was also abundant here, while another species of the same genus, *L. asper,* was represented by fewer specimens. The fulgorid, *Delphacodes albostriata,* was more abundant here than in the previous station. Both areas were represented by numerous Hymenoptera. Table 15 lists the species taken.

TABLE 14. Arthropods of Agropyron-Draba Associes—Station 20. L, larva; N, nymph; Y, young; A, adult.

Species	Week of				
	7/2	7/11	7/16	7/23	7/30
Elater sp.	1				
Aedes nearcticus	2				
Aedes punctor	1				
Aphis sp.	1	8		4	
Simulium vittatum	2	16	1		5
Exochus curvator	1				
Laevicephalus striatus	3N	64N 3A	9N 3A	6N 53A	3N 69A
Delphacodes campestris	1A	27N 2A	5N	1A	9N
Epiptera sp.	3N				
Chlamydatus pullus	4N				
Cantharis mandibularis		1			
Aedes sp.		2	1		7
Dasyneura sp.		3			
Dacnusa sp.		1			
Platygaster near *confusa*		33	5	4	
Habrocytus sp.		2	1	1	2
Simulium venustum		1	1		5
Simulium corbis		1			
Simulium subexcisum		1			
Chirothrips manicatus		2		3	1
Aeolothrips fasciatus		12			1
Thrips tabaci		2		2	4
Taeniothrips vulgatissimus		2			
Anaphothrips sp.		2			
Terebrantia		20N	2N	5N	
Adialytus sp.		1			
Apanteles sp.		2		1	1
Pteromalus sp.		2	2		1
Copidosoma sp.		1		2	1
Callimomus sp.		1			
Eurytoma sp.		3			
Lygus pratensis		8N 1A			
Nabis limbatus		5N 1A		1N 1A	
Delphacodes albostriatus		2N 2A	3A		
Araneus patagiatus		2			
Clubiona sp.		1Y			
Chelonus sp.			1		
Zootrephes sp.			1		
Terobia sp.			1		1
Hypopteromalus sp.			1		
Sphaerophoria nigratarsi				1	
Leiophron laevus				1	
Microgaster sp.				1	
Aptinothrips rufus				2	3
Xysticus bimaculatus				2	1
Capitophorus minor					3
Meniscus sp.					1
Endasys sp.					1
Homelys sp.					1
Trioxys sp.					
Pleurotropis sp.					1
Trigonogastra sp.					1
Necremnus sp.					1
Tenthredinid				1L	1L
Mites			9		
Chironomidae	5	64	19	74	379
Diptera	1	67	79	43	40
Total	25	368	144	209	544

TABLE 15. Arthropods of Draba-Cerastium Associes—Station 21. N, nymph; A, adult.

Species	Week of			
	7/11	7/16	7/23	7/30
Haltica tombacina	1			
Aedes sp.	5	9	3	1
Harmolita sp.	1			
Xanthosoma sp.	2			
Pteromalus sp.	1			
Simulium vittatum	6			
Simulium venustum	1		1	7
Simulium subexcisum	3			
Aeolothrips fasciatus	1			
Thrips near *madroni*	6			
Nabis limbatus	1N		1A	3A
Chlamydatus pullus	52N 13A	7A	12A	20A
Melanotrichus sp.	1			
Nysius sp.	36N	4N	18N 1A	12A
Laevicephalus striatus	100N	11N 2A	25N 46A	6N 118A
Laevicephalus asper	1A	4A	4A	5N 11A
Delphacodes albostriata	3N	2N	3N	2N
Delphacodes pellucida	1A		1A	
Sphaerophoria nigratarsi		1	1	
Prionellus sp.			1	
Simulium corbis			2	
Thrips tabaci			1	
Aphis sp.				1
Bracon solidaginis				1
Macrosteles near *sexnotata*				2A
Grapholita sp.				1
Torticidae				1
Trichoptera		1		2
Tenthredinid	1A			
Chironomidae	109	25	35	177
Diptera	120	93	18	32
Total	465	159	173	402

AQUATIC LIFE OF THE TUNDRA

STATION 1—MAN-MADE POOL

Pool 1 was a haven for numerous water birds. They soared back and forth above it, waded around its edges, and swam out upon it. The most abundant forms were several species of sandpipers (Fig. 17) and ducks. Apparently the main food item of these birds was chironomid larvae of which, on June 12, a red larva averaged 1000 per square foot of bottom, and a green larva averaged 100 per square foot. Hydracarina, mainly the species *Piona nodata latigenitalia,* reached their greatest abundance in this habitat and averaged about 300 per square foot of bottom surface.

By June 21 the water of the pool had receded six inches and chironomids were pupating and emerging. Larvae had increased to about 100 per square inch of bottom. Around the edges of the pool a species of dolichopodid (undetermined) ran upon the surface of the water in numbers of about one to ten square feet.

A week later sedges and rushes were growing in the shallowest edges of the pool, and algae were becoming thick in quiet places. The water had receded another two inches. During this period of observation there was a high wind and it was noted that insects ordinarily found upon the surface of the water were hiding in quiet places in and among masses of algae. Chironomid larvae were still the most abundant insects. Dytiscids (Fig. 20A) and their larvae were buried in the algae and numbered about four per square foot. With them were many caddis larvae, chironomid pupae, ten per square foot of algae, and corixids, four to a square foot of still water. An unidentified larva feeding upon dead insects that fell on the algae was pupating, forming odd club-shaped puparia. This puparium was expanded at the anal end to form a float so that the pupa would not sink and drown. Snails were laying eggs, were crawling among the strands of algae, and numbered 20 per square foot. At this time tipulids were emerging.

By July 5 algae had expanded to cover a larger part of the water surface. Daphnia, which were becoming abundant by June 28, were now very numerous. Young Piona appeared in the water in thousands. Branchinecta had become evident and was numerous. The fresh-water Turbellaria, *Mesostoma arctica,* had greatly increased in numbers, and snail eggs abounded. Beetle larvae, although of all ages, had grown considerably in size. So abundant was life in the pool at this time that it averaged about 80,000 macroscopic forms per cubic foot of water.

A week later the animal life was still of the same abundance. Branchinecta was full-grown and carrying eggs. It and Daphnia were the most numerous animals. Mesostoma and the club-shaped pupae were still in numbers. As the season progressed, the algae continued to invade more water area so that by July 19 it was present in large mats. Branchinecta did not appear to like this shaded water and was numerous only in open water. Daphnia seemed to show the same preference, but was also abundant under the algae. By now eggs of emerging chironomids had hatched and competition for room on the bottom of the pool was so great that their larval tubes were many-deep and formed a solid mat. Mesostoma was still abundant, but beetles were reduced in numbers, and no club-shaped pupae were evident. Many of the Hydracarina had become adults. On July 26 it was noted that this pool supported a beautiful crustacean which was found in no other pool within the vicinity of Churchill. This was *Lepidurus arcticus* (Fig. 18B), and its appearance in the water was localized in the deepest end of the pool where adults averaged one to ten square foot of bottom. Only very few immature specimens were taken, which indicated that they had been young earlier in the season and were now reaching adulthood. By this time the algae had continued its encroachment on the open water, and the small white bloom of *Batrachium divaricatum* was appearing. At a shallow end of the pool life was still in abundance of

80,000 or 100,000 individuals per cubic foot of water, and Daphnia made up the bulk of these. Branchinecta were much less numerous; beetle larvae were leaving the water to pupate; adult beetles were fewer, but corixid nymphs were becoming abundant.

On August 2, the day before departure from Churchill, it was noted that the algae had extended much farther into open water, and that *Caltha palustris* and the *Batrachium* sp. were blooming. On the surface of the water corixid nymphs were maturing and were the most conspicuous form. Adults were just beginning to appear. Daphnia were reduced in numbers, and there were but a few old Branchinecta, Lepidurus, and beetle larvae. Young snails were hatching prolifically. Species taken here included *Physa* sp., *Pionocercus* sp., *Stagnicola palustris nuttalliana, Coelambus hudsonicus, Callicorixa alaskensis, Colymbetes sculptilis, Hydroporus griseostriatus, Haliplus strigatus, Araneus patagiatus, Daphnia pulex, Simocephalus vetulus, Diaptomus arcticus, Branchinecta paludosa, Hydroporus jaror, Daphnia magna, Gerris pingreensis,* and the fish *Pygosteus pungitius.* Among these the beetles *Coelambus hudsonicus* and *Colybetes sculptilis;* the hydracarinid *Piona nodata latigenitalia; Lepidurus arcticus;* and *Daphnia magna* reached their greatest numbers in this pool. *Daphnia magna* appeared here only rarely and was not taken in other pools.

Station 8—Permanent Pool on High Tundra

Although this pool was protected by surrounding rocks, it did not maintain an alga flora (Fig. 15). There were but few sedges growing in the shallow parts. Table 16 lists the species taken and indicates by numbers those usually found after sweeping a Needham aquatic net through the water in a five-foot sweep stroke. On June 12 animal life on the bottom of the pool averaged about five snails, five beetle larvae, 200 ostracods, 20 hydra, 200 chironomid larvae, and three aquatic annelids per square foot.

On June 16 frogs, *Rana cantibrigensis,* were in abundance and were singing loudly. Chironomid larvae were still the most numerous form, and young Branchinecta were appearing in the water. A week later chironomids of an unidentified species were emerging rapidly, especially in small, quiet coves where they came from the water more than 1000 per square foot. Most of the Branchinecta had nearly doubled in size since the previous observation. June 30 found many of the Branchinecta adults and carrying eggs. The copepod, *Heterocope septentrionalis,* had made its appearance and was the most abundant form present. There was a decrease in the number of chironomids and an increase in annelids. The Branchinecta steadily decreased in numbers until on July 7 they were but a third as numerous as at the previous observation. At this time corixid nymphs and beetle larvae were conspicuous. July 14 found a few sedges along the edge of the pool in bloom, and among them in the water life was most abundant. Elsewhere animal life was reduced, and the

Table 16. Animal life from permanent pool—Station 8. N, nymph; A, adult; L, larva.

Species	Week of							
	6/12	6/16	6/24	6/30	7/7	7/14	7/21	7/28
Physa sp.	6		2		5	19	4	1
Gyraulus circumstriatus	5	2				10	2	
Agabus sp.	1L	1L	4L		2L	3L	3L	1L
Ilybius sp.	1L			5L				
Ostrocods	12							
Annelida	3	3	4	4	1	1	1	2
Hydroporus griseostriatus		1						
Coelambus hudsonicus		2						
Branchinecta paludosa		2	7	2	6	4	1	
Callicorixa noorvikensis		1A		2			23 N	9 N
Haliplus strigatus			2A&L		2A&L			
Heterocope septentrionalis			70	2	7	16	9	8
Arctocorixa convexa			1	1				
Hydroporus sp.				1L	1L		1L	
Agabus colymbus					1			
Colymbetes sp.					4L	7L	5L	
Simocephalus vetulus					2	4		
Placobdella phalera					1			
Agabus infuscatus						1	5	3
Hydroporus lapponum						2		
Baetis sp.						1 N		
Mesostoma arctica						2	3	1
Hydroporus arcticus							7	
Graphoderes sp.							1	
Diaptomus arcticus							3	2
Trichoptera				4L				
Chironomidae	6A		1000A	1A				
Chironomidae	49L	124L	28L	12L	14L	11L	3L	3L
Eelworm	3	2	1		1			
Corethra sp.					1L			
Total	86	138	1119	34	48	81	71	40

Branchinecta was gone, except for a few old individuals. On July 21 there were still a few Branchinecta, but Heterocope was the most abundant form in the water and Callicorixa nymphs on the surface. Beetles and their larvae were numerous among the sedges. At the last observation, on July 28, Branchinecta was gone, Heterocope fewer, and Callicorixa nymphs were numerous and nearly mature.

The snail, *Gyraulus circumstriatus,* was found most frequently in this pool. The leech, *Placobdella phalera,* was found only here but may have occurred at other pool stations and was overlooked.

Station 9—Pool Among Rocks

Where groups of rocks formed deep hollows, these hollows were often filled with water, making pools of various sizes, some temporary and others apparently permanent (Fig. 14). The pool selected for this station lasted during the entire period of observation and, although the water receded, it did not disappear rapidly enough to indicate that it would be dry before freezing weather. Neither this pool nor Pool 8

had an outlet. Pool 8 was supplied by drainage from the high tundra, but this pool was maintained through rainwater and melting ice. It contained no vegetation, and had only a small amount of organic detritus on its bed. The lichen, *Parmelia* sp., occurred over the surface of surrounding rocks down to a level at which the water regularly bathed the stone. On June 12 life in this pool was only about one fifth as abundant as that of Station 8. Beetles were absent. Four days later animal life was still low, with no beetles and only a few chironomids. During the third week of observation chironomid adults were emerging, but were only one tenth as abundant as in Station 8. Adult beetles were making their appearance, and first instar larvae were four per square foot. By June 30 animal life was increasing. A few Daphnia appeared, and beetle larvae were more abundant. Many of the remaining chironomid larvae were pupating. Seven days later Branchinecta eggs had hatched and the pool was alive with them. Caddis larvae had left the water in order to pupate. Swimming along the bottom were a few Corethra larvae. July 14, the Branchinecta were still abundant and were carrying egg pouches. A few Mesostoma were making their appearance and were producing eggs. Eggs from chironomids were hatching so that the larval tubes in the bottom were increasing. By July 21 the water level was down only five inches from its original depth. Branchinecta were fewer, while Daphnia had increased greatly. Adult beetles were making their appearance. At the last observation, on July 28, the water had receded six inches more. Now the water was dense with Daphnia. No estimate of the actual abundance was made, but they felt like grains when the hand was moved through the water. Beetles were now the most numerous of the season, and a few corixid nymphs had made their appearance. Identified species taken from this pool included: *Physa* sp., *Agabus* sp., *Callicorixa* sp., *Arctocorixa convexa, Hydroporus lapponum, Ilybius* sp., *Daphnia pulex, Branchinecta paludosa, Heterocope septentrionalis, Agabus infuscatus, Haliplus strigatus, Mesostoma arctica, Diaptomus arcticus,* and *Corethra* sp.

STATION 10—TEMPORARY POOL ON HIGH TUNDRA

A short distance from Pool 9 was Pool 10. It had an area of about 100 square feet and a depth of about two feet. Although it did not dry up in 1936, it probably was temporary in most years. At the time of the first observation there were a few beetles, but otherwise animal life was much less abundant than in Stations 8 and 9. On June 16 Caddis larvae had increased to one per ten square feet, beetles one to five square feet, and beetle larvae one to ten square feet. Chironomid larvae were becoming numerous on the bottom of the pool, and a few Branchinecta hovered there. On June 24 rushes and sedges were beginning to grow in the water. Life had rapidly become more abundant with the appearance of ten Corethra larvae to a square foot. Daphnia, beetles, and corixids were plentiful. Within a week Daphnia had become the most abundant form and Corethra was increasing. Other things were declining in numbers.

By July 7 the emergent vegetation had grown above the water level. Corethra was still more numerous, and there were a few remaining large Branchinecta. On July 14 it was found that rushes had grown to a foot above the water, and sedges were in bloom. By this time the two forms, Daphnia and Corethra, were the dominant animals. A week later rushes were in bud, while Corethra larvae were much fewer, and only a few Branchinecta remained. Heterocope had become abundant, and Daphnia still held its place of prominence.

The last week of observation found life much less abundant, with nearly all Corethra pupated. The water level was low and there were scarcely any Branchinecta. Heterocope and Daphnia were disappearing. Identified species collected here included: *Agabus punctulatus, Hydroporus melanocephalus, Cyclops vernalis, Agabus* sp., *Aedes* sp., *Stagnicola palustris nuttalliana, Branchinecta paludosa, Corethra* sp., *Agabus clavatus, Daphnia pulex, Coelambus* sp., *Hydroporus rufinosus, Pardosa* sp., *Callicorixa noorvikensis, Mesostoma arctica, Diaptomus arcticus, Baetis* sp., *Heterocope septentrionalis, Agabus infuscatus, Hydroporus lapponum, Dytiscus* sp. Among the forms present the beetle, *Hydroporus melanocephalus;* the snail, *Stagnicola palustris nuttalliana;* and the *Corethra* larvae were the most representative.

STATION 11—LAKE ANNABELLE

On the day of arrival, ice was just raising from the bottom of Lake Annabelle (Fig. 13). At this time corixid adults were actively swimming near the bottom of the lake and averaged about 100 per square foot. There were three species of corixids represented, and they and water beetles were in the ratio of ten corixids to one Hydroporus. There were ten Hydroporus to one Agabus. During the next week temperatures dropped below freezing and the water was again covered with ice. The insect population had greatly reduced, and chironomid larvae appeared only ten per square foot. In shallow parts of the lake algae occurred in small jellyfish-like masses. In these masses were represented *Pediastrum* sp., *Scenedesmus* sp., *Merismopedia* sp., and *Glaucocystus* sp. By June 17 ice was melting rapidly and the last of it raised from the bottom.

At the south end of the lake, where there was a dense border of willows, wave action had eaten about a foot underneath the sphagnum. Under this ledge were occasionally found Plecoptera nymphs of an unidentified species. Near the bank Collembola jumped about upon the water in numbers of about 15 per square foot. A week later small newly-hatched Branchinecta were making their appearance and numbered five per cubic foot of water. Nymphs of ephemerids, *Baetis brunneicolor* and *B. hudsonicus,* were taking the place of Plecoptera, but were few in number. By July 8 Branchinecta, Daphnia, and

Heterocope had become the most numerous organisms. On July 15 Branchinecta was full-grown, and it and Heterocope were numerous; but Daphnia had nearly disappeared. Baetis and a few beetle larvae appeared under the banks. A week later Branchinecta was in about the same abundance, while Baetis had completely replaced the Plecoptera nymphs. Heterocope was still abundant, but life appeared scarce in comparison to that of the pools.

On the last day of observation, July 29, it was noted that Branchinecta had increased in abundance and all were adults. Heterocope, a brilliant scarlet form, grew to a size considerably larger in the lake than those found in the pools. Swimming at the surface of the water were Gordiacea in numbers of nearly one to ten square feet. Table 17 lists the

TABLE 17. Animal life of Lake Annabelle—Station 11. L, larva; N, nymph; A, adult.

Species	WEEK OF								
	6/9	6/13	6/17	6/25	7/1	7/8	7/15	7/22	7/29
Agabus arcticus	2		2	2	1	1			
Hydroporus griseostriatus	6		1						
Pygosteus pungitius	4								
Callicorixa noorvikensis	10								
Callicorixa alaskensis	2		1	6					
Arctocorixa chancei	3								
Chironomidae		10L	1L	9L		6L	2L		
Heterocope septentrionalis		3			4	30	25	6	
Arpedium sp.			1						
Achorutes pseudarmatus			12						
Isotoma sp.			1						
Gyraulus circumstriatus			5						
Annelid			1						
Branchinecta paludosa				200	20	3	3	4	
Hydroporus melanocephalus				1					
Hydroporus lapponum				1					
Colymbetes sculptilis				2L					
Physa sp.				6			1		3
Daphnia pulex				11		10		5	
Haliplus strigatus					1				
Ilybius angustior						1			
Baetis sp.						2 N	4 N	5 N	3 N
Diaptomus tyrrelli								3	
Perlodidae			19 N	2 N	9 N	6 N			
Trichoptera			5L	3L	1L	4L		3L	1A
Gordiacea									1
Total	27	13	49	244	36	63	35	26	7

species taken at Lake Annabelle and indicates the numbers from four five-foot strokes of the aquatic net at each observation. Insects characterizing this aquatic station were the beetle, *Agabus arcticus*, the collembolan, *Achorutes pseudarmatus, Baetis brunneicolor, B. hudsonicus*, and a perlodid. The corixid, *Callicorixa noorvikensis*, occurred here and at Station 17.

STATION 14—TEMPORARY POOL IN MIXED TUNDRA

This pool of small area, only a few square feet, was in a low spot among the sedges and lichens on the mixed tundra, and had a fauna quite different from that of other aquatic stations. A snail, *Aplexa hypnorum*, was the most abundant and characteristic form. On June 11 mosquito larvae were present. By June 15 sedges had grown two inches out of the water. Mosquito larvae and beetles were numerous. A week later sedges had grown to six inches out of the water, and animal life had not changed greatly except for a reduction in beetles. By June 29 sedges were eight inches high, and the water was rapidly draining away. At this time no mosquito larvae were evident, having pupated and the adults emerged (Fig. 20B). Beetles, snails, *Cyclops vernalis*, and Collembola were numerous. The sedges were in bloom by the fifth week of observation, and at this time there was a reduction in abundance of all animals but the snails and beetles. Not much water was left on July 13, but this contained many snails, some small beetle larvae and Cyclops. On July 20 water was practically gone, but in the remaining soggy spots the beetles and snails were congregated.

At the last observation, on July 27, sedges were in seed and the pool had been refilled by rains; therefore animal life was much less concentrated. Table 18 lists the species taken and indicates the numbers collected by three short strokes of the aquatic net. Most of the species taken were characteristic of this type of habitat. Besides the snails there were the beetles *Hydroporus melanocephalus, Laccobius* sp., *Ochthebius holmbergi, Helophorus nitidulus*, and *Hydroporus rufinosus*; the mosquito larvae *Aedes nigromaculis* and *Aedes alpinus*; and the Collembolan *Isotomurus retardatus*. The staphylinid genus Stenus was most closely associated with this type of habitat.

STATION 17—FRESH-WATER POOL WITH STREAM FLOWING THROUGH IT

Station 17 was a small marsh of about an acre in extent with open water in the center and a stream flowing through it (Fig. 12). Water drained from the mixed tundra into this pool and thence from it to Churchill Bay. On June 15 croaking frogs were numerous averaging one to five square feet of water. Sedges and willows around the pool had not yet begun to grow. Floating in the water were several large tipulid larvae and rat-tail maggots which were apparently seeking a place to pupate. Among the other insects, beetles were two per square foot; corixids one to two square feet; and gerrids one to ten square feet. By June 22 the water level was down several inches. Insect life had increased and was as follows to one square foot of bottom: three corixids, three caddis larvae, two beetles, two Hydracarina, ten swimming chironomid larvae, and two gerrids. A week later emergent vegetation had begun to grow above the water surface. At this time it

TABLE 18. Animals of temporary pool—Station 14. L, larva; A, adult; Y, young.

Species	Week of							
	6/11	6/15	6/22	6/29	7/6	7/13	7/20	7/27
Aplexa hypnorum	15	24	108	54	52	33	26	33
Hydroporus melanocephalus	3	2	7	15	12	15	29	6
Ilybius sp.	1L		1L					
Laccobius sp.		2	3	9	2	3	4	
Ochthebius holmbergi		1					1	
Helophorus nitidulus		1		3	1			
Hydroporus rufinosus		1		3	1		7	
Agabus bicolor		1						
Aedes nigromaculis		1L						
Aedes alpinus		1L						
Aedes sp.		6L	9L	4L				
Piona nodata latigenitalia		1						
Cyclops vernalis		1		18	4	9	2	
Agabus sp.			2	6	1	3	1	
Aedes nearcticus			7A					
Thyas stolli			1	6		3		
Acercus sp.			2					
Hydrobius fuscipes				9				
Euaesthetus sp.				3				
Isotomurus retardatus				9				
Hydroporus sp.				6L	3L	15L	5L	3L
Stenus occidentalis				9		3		
Annelid					1	6	2	1
Micryphantidae					1Y			
Haliplus strigatus							2	
Lebertia setosa							1	
Trichoptera					1L			
Chironomid		1L		1L				
Fly	4L	1L						
Total	23	44	140	155	81	92	76	47

was apparent that chironomid larvae covered the bottom of the pool as in Station 1. Observations showed that one square foot of bottom bore one haliplid, four corixids, one dytiscid, four Piona, two Stagnicola, and two caddis larvae. Frogs had now laid their eggs and some were hatching. On July 6 sedges had begun to bloom. Numerous fish fry *(Pygosteus pungitius)* appeared and were darting through the water. There were no Branchinecta, but numerous large Daphnia. Beetle larvae had become plentiful. During the week of July 13 the young fish had grown considerably, and damsel flies, *Coenagrion resolutum,* were emerging. Corixid nymphs, which had appeared earlier, were much larger, and there were a few very large caddis larvae. Frog tadpoles were now evident.

A week later the water was alive with corixid nymphs. They and young gerrid nymphs were most conspicuous. The tadpoles were beginning to develop hind legs. A few large Daphnia appeared. During the last week of observation a brown scum of algae formed over the water. Corixids and gerris nymphs were nearly full-grown. Tipulid larvae were growing, and beetle larvae were leaving the water for pupation. There were but few beetles, and copepods were gone. Although the corixids were fewer, they still were the most conspicuous form. Tadpoles were larger, and the damsel fly had laid its eggs and was gone.

TABLE 19. Animals of permanent pool—Station 17. L, larva; N, nymph; A, adult; T, tadpole.

Species	Week of						
	6/15	6/22	6/29	7/6	7/13	7/20	7/27
Ilybiosoma bifaria	1						
Helophilus sp.	1L						
Eristalis sp.	1L						
Callicorixa alaskensis	1	5	5				
Arctocorixa convexa	2						
Gerris pingreensis	3		11	2			
Rana cantabrigensis	3			2T		1T	1T
Stagnicola palustris nuttalliana	1		2	1	2	2	3
Annelid	1		2	1	2		
Trichoptera larvae	1	3	7	4	3		1
Hydroporus rufinosus		2					
Haliplus strigatus		1	3		3	1	
Physa sp.		3	2	1			
Ilybius angustior			1	1		2	
Hydroporus near *striata*			1				
Gyrinus minutus			1				
Hydroporus melanocephalus			2				
Callicorixa noorvikensis			8				
Gyraulus circumstriatus			2	3	4	2	2
Piona nodata latigenitalia			1				
Prionocera sp.			1				
Coenagnion resolutum			1N	1A			
Agabus sp.				10L	12L	2L	2L
Callicorixa sp.				1	11	69	17
Glossiphoria fusca				1			
Coelambus hudsonicus					1		
Hydroporus griseostriatus					1		
Hydroporus sp.					1L		
Dytiscus sp.					1L		
Eurycercus lamellatus					2		
Simocephalus vetulus					1		
Stenus umbratilis					1		
Hydroporus arcticus						2	
Gerris marginatus						19 N	5N
Agabus antennatus							1
Bembidion vic. longulum							1
Chironomidae		7L	9L	6L	11L	6L	
Pygosteus pungitius			9	6	10	5	
Total	15	21	68	40	66	111	33

Table 19 lists the species taken in one five-foot sweep of the aquatic net at Station 17. Of these the most characteristic were the gerrids, *Gerris pingreensis* (Fig. 20D) and *Gerris marginatus;* the frog, *Rana cantabrigensis;* the whirligig beetle, *Gyrinus minutus;* the damsel fly, *Coenagrion resolutum;* and the staphylinid *Stenus imbratilis.*

SUMMARY

During the summer of 1936 an ecological study was made of the invertebrate fauna at Churchill, Manitoba, at the mouth of the Churchill River near

59° N. It is at a border line between the vast northern tundra and the transcontinental coniferous forest. Weekly collections were made at seven aquatic habitats and fourteen terrestrial habitats throughout the tundra and forest within a three-mile range of Churchill.

During the 55 days of observations the average air temperature was 11.6° C., with a range of –2°-33°. Relative humidity averaged 76%, with a wide range of variation. Weather for the summer was made up of 40% clear, 20% partly cloudy, 38% cloudy, and 17% rain. The tundra was swept by winds almost constantly with 36% strong winds (over 1000 feet per minute), 24% medium winds (500 to 1000 feet per minute), 31% light winds (less than 500 feet per minute), and only 8% calm during the period of observation. Weather conditions during a given day varied greatly, depending upon the exposure of the given habitat. The tundra surface maintained the highest temperatures because of its heat absorptive and retentive powers.

Dominant plants of the tundra were lichens, or reindeer mosses (Cetronia, Usnea, and Oodonia). These were accompanied by subdominant flowering plants such as Labrador tea *(Ledum palustre)*, cranberry *(Vaccinum vitis-ideae)*, and arctic heather *(Dryas integrifolia)*. The seasonal aspection of flowering began with the mountain saxifrage *(Saxifraga oppositefolia)*, which bloomed early in June and continued through 61 species of flowers, to the aquatic buttercup *(Batrachium divaricatum)*, which was blooming the first of August when the observations were closed.

Plant succession on the tundra followed at least ten lines of development. Stages in this development included Eriophorum sedge associes in low places, followed by dwarf arctic willows, and from the willows to mixed tundra (late sub-climax). Arenaria associes on sand followed by Agropyron-Draba associes on sand blended through an associes of Draba-Cerastium into mixed tundra. The black spruce-tamarack association was invading the tundra and was invaded by the tundra so that along its border both forest and tundra forms of plants were found. The climax condition of the tundra in this area apparently was that of the high granite ledges bordering Hudson Bay. Minor successional developments are discussed.

Some 50,000 specimens of invertebrates were collected, and these were identified by 63 specialists. Over 400 species were taken. The population trend of terrestrial insects was estimated by means of the sweep method. There was slight insect activity during the first week of June, but it increased steadily to a peak of numbers and activity during the week of July 12. Following this peak the abundance of insects gradually dropped and was continuing to do so at the close of the observations. Aquatic populations followed this same trend, with local variations at different pools.

A permanent man-made pool within Churchill was frequented by many water birds, was nearly covered by floating algae, and was characterized by the beetles, *Coelambus hudsonicus* and *Colymbetes sculptilis*, the hydracarinid, *Piona nodata latigenitalia*, the crustacean, *Lepidurus arcticus*, and the cladoceran, *Daphnia magna*. On the high tundra a large permanent pool had a fauna similar to that of other more temporary pools and was characterized by the snail, *Gyraulus circumstriatus*, and leech, *Placobdella phalera*. Near this large tundra pool was a smaller rock-bound pool of more temporary nature. It lacked emergent vegetation and had a limited fauna. The type of high tundra pool having the most individual fauna was a temporary one grown up with emergent vegetation. The representative species here were a beetle, *Hydroporus melanocephalus*, a snail, *Stagnicola palustris nuttalliana*, and a *Corethra* sp. larva.

On the mixed tundra were temporary pools that drained into small streams during dry weather and these were grown up with *Eriophorum* spp. Characterizing this type of habitat were a snail, *Aplexa hypnorum;* the beetles, *Hydroporus melanocephalus*, *Laccobius* sp., *Ochthebius holmbergi*, *Helophorus nitidulus*, and *Hydroporus rufinosus;* mosquito larvae, *Aedes nigromaculis* and *Aedes alpinus;* a collembolan, *Isotomurus retardatus*, and a staphylinid of the genus Stenus. In the area under observation water drained into a small marsh with open water and its identifying animals were a fish, *Pygosteus pungitius;* frog, *Rana cantabrigensis;* gerrids, *Gerris pingreensis* and *Gerris marginatus;* gyrinid, *Gyrinus minutus;* damsel fly, *Coenagrion resolutum;* and the staphylinid, *Stenus imbratilis*.

Lakes large enough to have wave action had representative fauna including a beetle, *Agabus arcticus;* collembolan, *Achorutes pseudarmatus;* mayflies, *Baetis brunneicolor* and *Baetis hudsonicus;* and an unidentified perlodid.

Many terrestrial animals, such as the bumblebees and blowflies, did not seem to be closely associated with any habitat, but less active types were usually found most abundant in some particular place. Most abundant in the dwarf arctic willow associes was the flea beetle, *Phyllodecta americana*, a noctuid, *Hillia iris*, and tenthredinid larvae. Mixed tundra was made up of many small types and did not have a characteristic fauna. The Eriophorum associes had a characteristic collembolan and hymenopteran fauna and the tipulids, *Prionocera* sp. and *Limnophila mcclureana*, were found here. Climax high tundra with southern exposure had a more luxuriant plant growth and here the collembolan, *Entomobrya nivalis*, reached its greatest abundance. High climax tundra exposed to north winds was less luxuriant and its conspicuous inhabitant was a running spider, *Pardosa* sp. Tide flats of Churchill Bay had eight representative species that included a carabid, *Dyschirius nigripes*, a saldid, *Salda littoralis*, two fulgorids of the genus Delphacodes, three leafhoppers

of genus Macrosteles, and an anthocorid, *Teratocoris herbaticus.* Isolated clumps of black spruce in tundra supported a spider fauna that included *Araneus patagiatus* and *Pityohyphantes limitanea.* The black spruce-tamarack forest several miles inland from Churchill had a characteristic fauna of six species of dragon flies, the grasshopper, *Melanoplus borealis borealis,* and several species of chermids.

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CARABIDAE OF MOUNTAINS AND ISLANDS: DATA ON THE EVOLUTION OF ISOLATED FAUNAS, AND ON ATROPHY OF WINGS

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CARABIDAE OF MOUNTAINS AND ISLANDS: DATA ON THE EVOLUTION OF ISOLATED FAUNAS, AND ON ATROPHY OF WINGS

INTRODUCTION

Eighty-eight years ago Wollaston (1854) discovered that more than a third of the native beetles of the island of Madeira were flightless, with atrophied wings. Darwin soon, in *Origin of Species* (1859),* offered an explanation, that flying beetles tend to be blown away from islands and to perish in the sea, leaving flightless forms to survive and to evolve in the exposed environment. Jackson (1928, pp. 722-4) summarizes pertinent contributions and opinions of later authors.

Most modern entomologists believe that flightless beetles do predominate on remote islands, and on mountain tops, but the belief rests on scanty evidence. Island and mountain faunas are little known, and less is known of how they compare with normal, continental, lowland faunas. And why so many island and mountain species are flightless is still a disputed problem. One thing, however, is clear: Darwin's explanation was too simple. The problem is a complex one which cannot be solved by generalities but only by careful analysis of exact data.

In the following pages I shall present and attempt to analyze data, collected during the past 19 years, on beetles of one family, the Carabidae, as they occur on specific mountains and islands. In order to understand the mountain and island faunas, it will be necessary first to know a good deal about Carabidae in general and about continental Carabid faunas, and to discuss certain topics in ecology and evolution. The Carabidae are, of course, a special case, but much of what is found out about them should apply, with modification, to other beetles and to other insects.

I am by profession a museum curator and taxonomist, especially of Carabidae, so that this paper is a contribution from a museum and by a taxonomist to what is essentially an ecological and evolutionary problem. It would hardly be possible to attack the problem with any hope of success without a good museum collection for reference or without taxonomic knowledge.

I am indebted to Prof. Alfred E. Emerson, who is himself interested in causes and processes of organic atrophy, for numerous useful criticisms and suggestions, and to Mr. C. T. Bodwell and Prof. Stephen Taber for permission to reproduce the photographs in Figures 5 and 6 respectively.

I. WHAT ARE CARABIDAE?

Carabidae, or "ground beetles," are typically unspecialized, active, ground-living, predaceous beetles. Nearly 20,000 species are known. They are abundant on all continents except the Antarctic, and on most islands, and in all climates from the tropics to the Arctic. Most are nocturnal; a few, diurnal. A few are phytophagous and a few myrmecophilous, and the larvae of a few are parasitic on other insects, but most Carabidae appear to be rather simple predators, preying both as larvae and as adults on insects and other invertebrates. Their distribution is not usually limited by dependence on specific hosts.

Carabidae occupy diverse habitats. Most species do live on the ground. Many ground-living forms inhabit arid deserts, or open plains, or dry woods, or wet forests, without being associated with open water. They are all *geophiles*. Many other ground-living Carabidae are specifically associated with the banks of rapid brooks, slow rivers, or ponds, or with swamps, or just with very wet places, although none is completely aquatic. They are all *hydrophiles*. Finally, some Carabidae, especially in the tropics, are *arboreal*. These three ecological groups—geophiles, hydrophiles, and arboreal forms—are not sharply defined. Some geophiles are also facultative hydrophiles, occasionally but not specifically associated with open water, and some ground-living species are partly arboreal. But doubtful species are few. The ecological classifications given in this paper are good approximations.

Wings of Carabidae (Darlington 1936) may be fully developed, longer than elytra, complexly folded beneath elytra when not in use, and suitable for flight, c apparently so; or wings may be reduced, shorter than elytra, often minutely vestigial, and not suitable for flight. Carabidae with full wings, apparently suitable for flight, are *+winged;* those with reduced or vestigial wings, not suitable for flight, are *—winged.*

This paper necessarily deals with wing-state of Carabidae, not directly with flight and flightlessness. Little is known of the actual flight of rare or exotic species. A few diverse insects, including some Chrysomelid and Curculionid beetles, have +wings but lack muscles necessary for flight (Jackson 1933, esp. pp. 733-5). Some +winged Carabidae, too, may be incapable of flight. But many Carabidae do fly well, and it is probable that most +winged species do so. The —winged species, of course, are all flightless.

All Carabidae are descended from +winged ancestors, and a majority of existing species are +winged, but —winged species make up a considerable minority: 20% of all species in eastern North America, 12% to 15% in South America, and 45% in Australia (see Section II, below, for references and data). From these figures and from what I

* See "Beetles, wingless, in Madeira" in index of this or later editions of the *Origin*.

know of Carabid faunas elsewhere, I estimate that of all species of Carabidae of the world one fifth or one quarter are —winged. But in limited areas the proportion of —winged species will average less than this (Fig. 1).

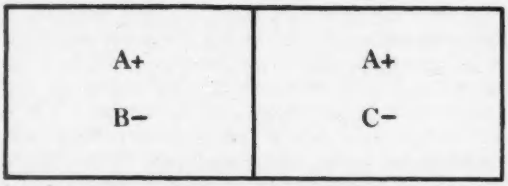

Fig. 1. Diagram to show why —winged species are proportionately fewer in small than in large areas. A+ is a +winged species occupying a large area; B— and C—, different —winged species in different halves of the same area. Proportion of —winged species in whole area is 67%; in each half, 50%. An effect of this sort has been found among Carabidae in eastern North America (Darlington 1936, p. 162) and in Australia (Section II, below). It reflects the relatively low powers of dispersal of —winged forms, and their tendency to set off local endemic species.

Occurrence of +winged and —winged Carabidae is not random, but is correlated with locality and with habitat. There are localities where all known Carabidae are +winged, *e.g.* in wet lowland rain-forest at Barro Colorado, Panama (76 species), and localities where all are —winged, *e.g.* in wet mountain rain-forest on Pico Turquino, Cuba (7 species). As to habitats, arboreal Carabidae *and hydrophiles* are almost always +winged; —winged species occur chiefly among geophiles. I have found this correlation in Australia as well as in North America, and it is indicated elsewhere. It is one of the most important facts in ecology of Carabidae of the world.

A few Carabidae, usually geophiles, have dimorphic wings, and are conveniently designated *±winged* (plus or minus winged). Such species make up at least 5% of all Carabidae of New Hampshire and 9% of those of Scandinavia, where 28 species are ±winged (Lindroth 1939, p. 258). Comparable numbers of dimorphic species are to be expected elsewhere in the colder parts of the northern hemisphere. They seem to be fewer in other parts of the world, but scattered dimorphic species are known from every continent and from Cuba, the Hawaiian Islands, and the Seychelles.

Wing dimorphism of Carabidae usually involves the existence in single populations of two sorts of individuals, one +winged, the other with wings uniformly or variably reduced. The dimorphism is usually not sexual, not seasonal, and not primarily geographical. But geographical differentiation of wings does occasionally occur, and sometimes seems to reflect adaptation to special environments (Figs. 2, 3). The +winged individuals of some dimorphic species are known to be able to fly; the —winged individuals, of course, cannot.

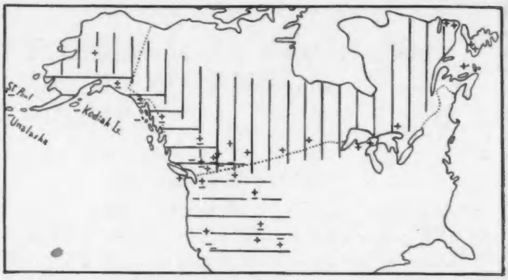

Fig. 2. Geographical differentiation of wings of *Patrobus fossifrons* (Esch.) (from Darlington 1938a). Three subspecies are distinguished by slight genitalic differences and by state of wings (localities of +winged and —winged specimens of all subspecies are marked by +'s and —'s on map). *P. f. fossifrons*, on St. Paul, Unalaska, and Kodiak Islands, is —winged (60 specimens); *P. f. dimorphicus*, of southern continental Alaska to northern California and Colorado (horizontal lines) is ±winged (160 specimens, about ¼ +winged, ¾ —winged); *P. f. stygicus*, of north-central and northeastern North America (vertical lines) is +winged (93 specimens). The ±winged western population is presumably ancestral; the —winged island populations *may* have evolved by selection in an exposed habitat; the +winged central and eastern population may have evolved by selection during active migration into country part of which was uncovered by ice sheets only a few thousand years ago.

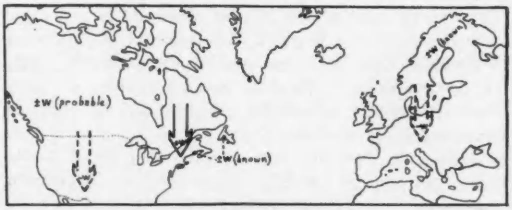

Fig. 3. Geographical differentiation of wings of *Notiophilus aquaticus* (L.). Species is circumpolar or nearly so, and is known to be ±winged in northern Scandinavia (Lindroth, in letter) and in northeastern North America (of 30 specimens examined from Massachusetts to Newfoundland, 27 are +winged, only 3 —winged, 1 from Maine, 2 from Newfoundland). On mountains of central Europe and on the Rocky Mts. of Colorado and New Mexico the species is apparently entirely —winged (small series seen). But on the Presidential Range in New Hampshire only +winged individuals have been found, occurring erratically. (State of wings of the species in Asia is unknown.) Probable explanation: a ±winged ancestral population is widely distributed in northern regions. Sub-populations derived from it have reached the mountains of central Europe and western North America and become —winged (broken arrows). But on the Presidential Range (solid arrow) the species is not established and only occasional, +winged, immigrant individuals occur.

Carabidae, then, are numerous, widely distributed in diverse habitats, predaceous and usually independent of specific hosts. Their wings vary, and state of wings is strongly correlated with locality and habitat. For these reasons, Carabidae are very good subjects for study of evolution of flightless faunas in special habitats on mountains and islands.

II. CONTINENTAL FAUNAS

NUMBERS OF SPECIES IN CONTINENTAL AREAS

In eastern North America, Carabidae are most numerous in the Carolinian zone, from the latitude of New Jersey and Indiana to the Carolinas. New Jersey, about 7,500 sq. mi. in area, with no high mountains, is credited with some 353 species of Carabidae (Smith 1910). Indiana, about 36,000 sq. mi., no mountains, has some 366 species (Blatchley 1910). North Carolina, about 48,000 sq. mi., extensive mountains, is provisionally credited with 351 species, of which perhaps 300 are found in the lowlands and lower hills, but this number will be increased by further collecting. "District of Columbia" (within 20-mile radius of the Capitol), about 1,250 sq. mi., no mountains, has some 304 species (Ulke 1902). In the optimum, moderate temperate climate of the Carolinian Zone of eastern North America, then, more than 300 species of Carabidae occur in limited lowland areas.

North of the Carolinian Zone, Carabidae decrease in number. New Hampshire, about 9,000 sq. mi., some mountains, possesses 298 species, of which 265 comprise the lowland fauna (see below). Actually, the number of species decreases rapidly within the state as one goes northward. Labrador is credited with only 46 species (Sherman 1910), although a few more probably occur.

Southward, too, in subtropical and tropical areas, Carabidae appear to decrease in number. Florida, about 55,000 sq. mi., no mountains, has only some 248 species (Leng 1915). The American tropics probably have still fewer species, perhaps 200, or a few more, in limited but diverse lowland areas. No exact figures are available, but certainly Carabidae make up a much smaller fraction *of the whole insect fauna* in tropical than in north-temperate America.

ECOLOGY AND WINGS OF CONTINENTAL CARABIDAE

In *cool-temperate North America* (in New Hampshire and in Colorado, and probably elsewhere in similar faunal zones) Carabidae are nearly 2/3 geophiles, about 1/3 hydrophiles, not much over 5% arboreal. As to wings, in eastern North America Carabidae are about 20% —winged, 4% ±winged, 76% +winged (Darlington 1936, slightly revised). But —winged species are relatively fewer in limited areas (Fig. 1). All the —winged and ±winged species are geophiles; strict hydrophiles and arboreal species seem all to be +winged.

In *tropical American lowlands* Carabidae are not quite 1/4 geophiles, at least 1/2 hydrophiles, nearly 1/4 arboreal. These are the proportions among 134 species (a good, but not complete sample of the fauna) taken by myself in ecologically diverse lowlands south of Santa Marta, Colombia, northern South America, during 14 months' residence as entomologist for the Colombia Division of the United Fruit Co. Smaller samples from other localities suggest that these proportions hold at least approximately elsewhere in lowland, tropical America. As to wings, almost all lowland, tropical American Carabidae are +winged. Of the 134 Santa Marta species, 132 are +winged, only 2 —winged; of 76 species from Barro Colorado, Panama (incomplete sample), all are +winged; and practically all Carabidae of lowland tropical habitats in the West Indies are +winged (see below). But note: in the highlands of South America, and in the temperate zone south of the tropics, —winged stocks are much more numerous. A brief survey of about 575 species from different parts of South America in the Museum of Comparative Zoölogy indicates that 12% to 15% of all Carabidae of the continent are —winged, the proportion being much smaller in the tropical and larger in the temperate areas.

In *Australia*, Carabidae are at least 1/2 geophiles, not quite 1/4 hydrophiles, not quite 1/4 arboreal. This estimate is based on a manuscript list of 1,592 known Australian Carabidae, and on a year's personal experience collecting with the Harvard Australian Expedition of 1931-32. Most of the arboreal species are confined to a peculiar local habitat: the shaggy trunks of eucalyptus and other Australian trees. Without the tree-trunk fauna, Australian Carabidae are nearly 3/4 geophiles, at least 1/4 hydrophiles, very few arboreal. As to wings, so far as I can determine from my list and from examination of over 600 species in the Museum of Comparative Zoölogy, nearly 45% of Australian Carabidae are —winged. Almost all the hydrophiles and arboreal forms are +winged, but about 75% of the geophiles are —winged. Again the proportion of —winged species is less in limited areas (Fig. 1). For example, from a small but diverse lowland area in southwestern Australia we possess a sample of 68 species of Carabidae, most taken by myself at Perth, Bridgetown, Margaret River, Pemberton, etc., and including 36 geophiles (19—, 1±, 16 +winged), 14 hydrophiles (2—, 12 + winged), 18 arboreal, most on tree trunks (all +winged). The dimorphic species is *Scopodes sigillatus*. The —winged hydrophiles are species of Coptocarpus.

TEMPERATE AND TROPICAL CARABID FAUNAS

Temperate and tropical Carabid faunas, as described above, differ rather strikingly. Temperate faunas, in North America, include more species than tropical faunas. Temperate faunas consist of many geophiles, fair numbers of hydrophiles, but few arboreal species. Tropical faunas consist of fewer geophiles, more hydrophiles, and numerous arboreal species. And in temperate faunas many geophiles are —winged, while in tropical faunas, at least in America, most Carabidae of every sort are +winged. These differences are diagramed in Figure 4, and briefly discussed thereunder.

These generalities are based on Carabid faunas of few regions. Comparable data on the faunas of other regions are much needed. It is safe to say, however, that continental Carabid faunas do vary consider-

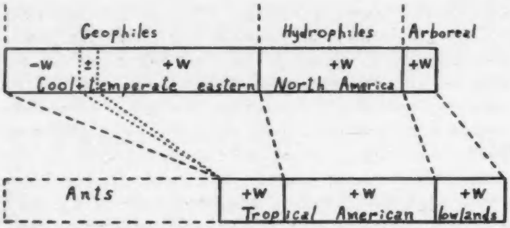

FIG. 4. Diagram to compare the Carabid faunas of cool-temperate eastern North America and of tropical American lowlands (see text). Diagram is intended to suggest that the tropical fauna would be larger than the temperate fauna if it were not for competition with ants, which are numerous and aggressive in the tropics. The tropical fauna is deficient in geophiles, especially in —winged species, which come into close competition with ants, but is rich in hydrophiles which inhabit swamps and stream-banks where ants are few, and rich in arboreal species, which compete with ants but which may derive special advantage from ability to fly. Note, however, that other factors, including temperature, may be partly responsible for differences between temperate and tropical faunas (see p. 51).

ably in number of species, in ecology, and in state of wings. By proper comparison of different faunas it will be possible to find out a good deal about why Carabidae fly and about factors concerned in wing atrophy. And, obviously, it will be necessary to know rather accurately the nature of the particular continental or lowland fauna from which an island or mountain fauna has been derived in order to understand the latter's evolution.

III. EFFECT OF LIMITATION OF AREA ON CARABIDAE

Limitation of area often limits both number and kind of species of animals in isolated faunas. Very small islands, for example, regardless of their origin, support few species, and the species are usually small or sedentary forms, such as insects and land snails, which are fit to exist in small areas. This is obvious.

How limitation of area exerts its effect is not so obvious, but presumably it acts in an orderly way to produce orderly correlations between area, number of species, and kind of species in different, comparable faunas. Correlations between area and number of species have occasionally been noticed. For instance Dunn (1934) lists the numbers of species of reptiles and amphibians on several small West Indian islands, and finds, ". . . these small islands harbor fewer genera and species than either the Greater Antilles or South America. Islands of approximately the same size but of very diverse histories do not differ quantitatively, but islands of different sizes have species in direct ratio to size and elevation."

Carabidae, too, show correlations between area, number of species, and probably kind of species. Continental areas are inhabited by many, diverse Carabidae; islands, by fewer, less diverse forms; very small islands, by very few species indeed, or by none. The exact relation is difficult to discover. It is difficult to find areas, sufficiently isolated to support independent faunas, which differ in extent but which are otherwise comparable in nature and history. Perhaps no set of areas fully answers these requirements, but the four islands of the Greater Antilles, in the West Indies, come near to doing so. The islands are ecologically similar, each diverse, each with lowlands and local or extensive mountains, with similar climates, and with Carabid faunas which are generally similar in composition and origin, and reasonably well known. Cuba, nearest the continent, is in the best position to receive immigrants, but even mammals, so far as they have reached the Greater Antilles at all, have in the past dispersed freely between Cuba, Hispaniola, and Puerto Rico (Darlington 1938, p. 288), and active +winged Carabidae such as make up most of the West Indian fauna must have been able to disperse freely along the same route. The area of each island, the nature of its mountains, and the number of species of Carabidae known from it are summarized in Table 1.

TABLE 1. Correlation between area, mountainousness, and number of species of Carabidae known from islands of the Greater Antilles.

Island	Approx. area in sq. mi.	Mountains on island	Total species Carabidae	Lowland species	Strict mountain species
Cuba	40,000	local, part recent	163	144	19
Hispaniola	30,000	extensive, high, old	148	97	51
Jamaica	4,500	moderate extent, old	80	63	17
Puerto Rico	3,400	extensive, but low	68	60	8

Table 1 shows that the number of species of Carabidae on Greater Antillean islands does vary with area. Even Cuba, the largest island (40,000 sq. mi.), has fewer species than similar areas on continents. Puerto Rico (3,400 sq. mi.) has less than half as many species as Cuba. Smaller islands in the West Indies certainly have fewer species still, although exact figures are not available. Inspection of Table 1 suggests that, among the Greater Antilles, division of area by 10 divides number of species of Carabidae by 2. But this is at best a rough approximation, and the ratio might be different among much larger or much smaller islands.

The relation between area and number of species of Carabidae is *not* due primarily to multiplication of species in different parts of large islands. In one small lowland area in Cuba, within a radius of about 5 miles of Soledad Central in southern Santa Clara Province, 100 species of Carabidae, practically all widely distributed elsewhere in Cuba, are already known—more than are known from all of Puerto Rico—and probably several times as many as exist

independently on any low island of 5-mile radius anywhere in the world. The number of species which occur *together* in limited areas of an island somehow depends on the area of the whole island. Similarly, the number of species which occur together in limited areas of a continent depends on the large area of the continent. It has been found (Section II) that nearly as many species of Carabidae (over 300) occur in an area of 1,250 sq. mi. near Washington, D. C., as in 7,500 sq. mi. in New Jersey or 36,000 in Indiana. These limited areas have large, diverse, nearly similar Carabid faunas only because each is part of the much larger, fairly homogeneous area of continental eastern North America.

Total area available, then, is an important factor in determining the number of species which occur together in Carabid faunas. Limitation of area limits the number. This must be partly an effect of limitation of habitats. On small islands, for example, absence of rivers excludes a certain number of hydrophile Carabidae and reduces the total of island species. But limitation of habitats is not the whole explanation. Puerto Rico is as diverse as Cuba, so far as Carabid habitats go, but supports less than half as many species, and some much smaller islands, with still fewer Carabidae, are ecologically diverse, except for absence of large streams. A more important effect of area on Carabid faunas is probably this: that large areas tend to be inhabited by many species, with sparse and somewhat unstable populations; small areas, by fewer species, with denser and more stable populations. Probably only species which maintain relatively dense and stable populations can exist permanently and independently in small areas—other species never become established at all, or are gradually eliminated. And where each species must maintain a dense and stable population, there is room for few species.

Limitation of area may be expected to affect the nature as well as the number of species of Carabidae in isolated faunas. Some effect must again be due to limitation of habitats, *e.g.* absence of rivers on small islands, by excluding certain sorts of hydrophiles, definitely modifies island faunas. Straggling of flying species away from small areas may eliminate certain kinds of species (but see later sections). But also, and more important, as limitation of area modifies populations it may have a profound effect on usefulness of flight and state of wings of Carabidae, as will be shown at the end of the next section.

IV. ROLE OF FLIGHT, NATURE OF POPULATIONS, AND WING CORRELATIONS OF CARABIDAE*

In order to understand flightlessness, it is necessary first to understand the rôle of flight among Carabidae.

Some Carabidae fly for special reasons. Hydrophiles fly to escape rising water; arboreal species, to stay in vegetation above the ground. These sorts of Carabidae depend on flight and rarely lose their wings. But ordinary, ground-living Carabidae (geophiles) make no such special use of flight. They fly comparatively rarely, do not hunt their food on the wing, and usually do not fly to escape enemies, but run or hide instead. There is no obvious reason why most individual geophiles should need to fly at all, and many geophile species have, of course, become flightless. Nevertheless, a majority of geophile Carabidae in most parts of the world do retain their wings and do fly occasionally. Flight is apparently of some use to them. Probably it enables them to exist in certain sorts of ranges, to maintain sparse or scattered, unstable populations in large, unstable areas.

Collectors and ecologists know that species of animals which range over large areas are usually not evenly distributed, but exist in specific habitats at numerous, scattered, unconnected stations. They live as though on a checkerboard on which only scattered squares are habitable. And they are more or less unstable on the board. They do not necessarily maintain permanent populations on any single squares. But they maintain themselves on the board as a whole by continual, active dispersal of individuals, by continual repopulation of disinhabited squares and invasion of new ones. Such species have populations which are both scattered and unstable. And the areas which they inhabit are unstable too; habitable squares continually shift as a result of accident, erosion, ecological succession, or climatic changes. Maintenance of scattered, unstable populations in large, unstable, checkerboard areas must be greatly facilitated by flight. Even if individuals make no special use of flight, flight may still be useful periodically, for dispersal, repopulation, and maintenance of populations, and wings may be retained in species by periodic selection of flying individuals.

To turn for purposes of illustration from Carabidae to other, better-known insects: our common potato beetle, *Leptinotarsa decemlineata*, could probably exist indefinitely without flying if it were permitted to live undisturbed in stable, permanent potato fields. A number of related chrysomelid beetles are flightless, *e.g.* most Timarcha and some Chrysomela in Europe. But the potato beetle is not permitted to live undisturbed, and potato fields are neither stable nor permanent, so the beetle must and does maintain a scattered, unstable population in a series of unstable fields scattered over a large area, and it depends on flight to do so.

Another, better example is *Sitona hispidula*, a European weevil which feeds on clovers and related plants. Jackson (1928, 1933) finds that this insect is dimorphically winged; that +wings and —wings appear to be inherited in Mendelian fashion (with —wings dominant); and that many +winged individuals fly at least in the fall. The flight muscles usually degenerate during the winter, in hibernation. Both +winged and —winged forms are widely distributed in Europe. They often occur together, but Jackson found indications that +winged individuals

* *Cf.* Darlington 1936, pp. 156-164.

predominate in new, recently colonized places; —winged ones, in places where the species has long been established. Apparently this beetle disperses by flight, so that +winged, flying individuals have an advantage and are more numerous in new and probably in unstable regions, while —winged individuals have the advantage and increase in number in stable, favorable regions. And this is borne out by Jackson's observation that —winged individuals are more viable than +winged ones in the laboratory.

In these examples, the principal function of flight is to spread and maintain scattered, unstable populations in large, unstable areas. Probably, as suggested above, this is the principal function of flight also among most geophile Carabidae, which have no other obvious reason to fly, and which often become —winged and flightless.

It is significant that, at least within the temperate zones, —winged species are most numerous in the most stable regions, where flight has been least needed to maintain ranges. In northeastern North America, ecologically unstable during Pleistocene glaciations, few more than 30% of all geophiles, and only about 17% in some limited areas (lowlands of New Hampshire), are —winged. In Australia, relatively stable, with no recent continental ice, perhaps 75% of all geophiles, and more than 50% in some limited lowland areas (southwestern Australia), are —winged. (Figures from data given elsewhere in this paper.) Moreover, ±winged Carabidae are exceptionally numerous in cool northern regions (5% of all Carabidae in New Hampshire, 9% in Scandinavia), and this suggests that many species in the northern fauna are in transition from a +winged state adapted to the unstable late Pleistocene toward a —winged state adapted to more stable and favorable times.

A general correlation exists, too, between climate and wings of Carabidae. In temperate regions, —winged species are numerous; in the American tropics, very few. There are several possible explanations of this fact. Competition with ants may eliminate —winged forms in the tropics (Fig. 4). Tropical species may exist in populations so sparse as to require flight for their maintenance. Or warmth, especially at night, may give +winged flying forms a special advantage in the tropics (see *temperature,* Section VII). Certainly, for some reason, flight must be more useful to tropical than to temperate Carabidae.

It has been shown in Section III that small, isolated areas are inhabited by comparatively few Carabid species, each of which probably maintains a relatively dense and stable population. It has been found in the present section that maintenance of sparse or scattered, unstable populations in large, unstable areas is an important function of flight among Carabidae, apparently the principal function among geophiles at least in temperate regions. It follows that flight should tend to lose its function, permitting existence of flightless —winged species, especially of geophiles, in small, stable, temperate areas.

V. WING ATROPHY OF CARABIDAE*

As shown in the preceding section, use of flight and state of wings vary enormously among different Carabidae and under different conditions even in lowland continental regions. Flight is observably useful to hydrophiles and arboreal Carabidae, which are usually +winged; less useful (but not necessarily harmful) to geophiles, which are often —winged. Flight is useful (to maintain ranges) to species with scattered, unstable populations, which are usually +winged; less useful (but not necessarily harmful) to species with denser, more stable populations, which are probably more often —winged. Flight is useful in unstable regions, where most Carabidae are +winged; less useful (but not necessarily harmful) in stable regions, where more species are —winged. Flight is apparently useful to Carabidae in the hot tropics, where practically all species are +winged; less useful (but not necessarily harmful) in cool temperate regions, where many are —winged. And probably flight is more useful and Carabidae more often + winged in large than in small areas, where flight is less useful and *may* cause harmful straggling. These are not fixed nor complete correlations, of course, but are overlapping, partly interdependent, observed or deduced tendencies. Note that in most cases +wingedness is correlated with factors which make flight observably or presumably useful; —wingedness, with factors which reduce usefulness of flight but do not necessarily make it harmful.

Wing atrophy of Carabidae presumably begins with mutation; —winged mutants probably appear rather frequently in +winged stocks. When mutations appear, Carabidae probably keep or lose their wings chiefly by selection based on usefulness of flight. When flight is useful, in activity of individuals or in maintenance of populations, flying forms have a constant or periodic selective advantage, and +wings are maintained. When flight is not useful, the selective advantage shifts. If flight becomes harmful, the advantage shifts to flightless individuals, which may or may not be —winged. If flight becomes useless but not actually harmful, the advantage probably shifts directly to —winged individuals, not because they are flightless, but because they are inherently better, more viable insects, with simpler structure, simpler metamorphosis, and lower energy requirements than + winged forms. Remember that Jackson (1928) found —winged individuals of the weevil *Sitona hispidula* more viable than +winged ones, although —winged mutant Drosophila are usually less viable than the normal +winged form. Since it appears that Carabid wings atrophy where flight tends to become useless but not necessarily harmful, it is reasonable that inherent

* See again Darlington 1936, pp. 164-173.

superiority and selective advantage of —wingedness is an important factor in the atrophy process.

It is conceivable that heterozygous individuals, if —winged, might be inherently even more viable than pure, homozygous —winged forms, and this would tend to maintain ±winged populations indefinitely, but this appears not to be the case among Carabidae, among which ±winged populations are most common in recent, evolving (postglacial) faunas rather than in old faunas which are nearer equilibrium.

Although selection is presumably the chief process in atrophy of Carabid wings, certain other, non-selective, genetic processes may be involved too. Recurrence and accumulation of mutations may alone cause atrophy over long periods of time (discussed in connection with atrophy of Carabid wings by Darlington 1936). Prof. Alfred Emerson has called my attention to another process, suggested by Wright (1929, pp. 276-7). Genes often have multiple effects on many different organs. A given gene mutation which has a selective advantage because of its effect on one organ is likely to have secondary, random effects on other organs not under selection. Random effects of mutations are usually destructive. So evolution of certain organs by mutation and selection is likely to be accompanied by secondary, usually destructive changes (atrophy) in other organs which have no selective importance but are affected by the same genes.

Really, two stages should be distinguished in atrophy of Carabid wings. First is the change from +winged to —winged condition, which usually involves loss of ability to fly. So great a change must usually have a selective significance overshadowing gradual genetic processes, although the latter may play some part. Second is progressive atrophy of the wing vestiges, which apparently decrease in size in old —winged stocks, but which rarely or never disappear entirely (Darlington 1936, pp. 137-9). In this second stage of wing atrophy, recurrent mutation and secondary effects of evolution of other organs may be very important. Prof. Emerson suggests (in conversation) that the extraordinary persistence of wing vestiges in Carabidae may be due to the complex way in which the vestiges are tied to other organs by multiple effects of genes.

This and the preceding section should have made it clear that no one thing is uniquely important in determining wing-state of Carabidae. Many factors and perhaps several processes combine in complex ways to determine (1) whether or not flight is useful to the insects, and (2) whether +wings are retained or lost. The factors are often closely balanced, so closely that change in any one will change or reverse the sum of all, shifting the selective advantage from +wings to —wings or vice versa, causing, or inhibiting, wing atrophy.

This conclusion has been reached by study and comparison of Carabidae and Carabid faunas chiefly of lowland continental regions. It has now to be applied to Carabidae of mountains and islands.

VI. MOUNTAIN FAUNAS: DATA

PRESIDENTIAL RANGE, WHITE MOUNTAINS, NEW HAMPSHIRE

The Presidential Range, in the White Mts. of New Hampshire, is a mountain ridge about 10 miles long (Fig. 5). The ridge itself runs at an altitude of about 5,000 ft. above sea level, but from it rise several peaks of which the highest, Mt. Washington, reaches 6,288 ft. The highest surrounding valleys lie at about 2,000 ft. The slopes of the ridge are covered with Canadian and Hudsonian *forest* up to timber line, at about 4,500 ft. Above timber line, the ground is open, *exposed*, rocky in some places, grassy or mossy in others, with thickets of stunted trees only in sheltered corners, and with an Arctic-Alpine climate.

The Presidential Range, like all New Hampshire, was probably covered by the last Pleistocene ice sheet less than 20,000 years ago, and local glaciers have existed on the mountains still more recently. The topography of the range is recent, postglacial, with high, flat-bottomed glacial valleys, and with many small ponds and bogs in depressions carved out by ice both above and below the present timber line. The ponds and bogs are disappearing, of course. Now that the ice is gone, erosion is cutting down the glacial valleys and will eventually drain all standing water, and the mountains will slowly evolve a topography like that of unglaciated ranges, with deep, V-shaped valleys, uniformly steep slopes, and direct, rapid streams.

The fauna of the Presidential Range, and of all New Hampshire, is recent, post-Pleistocene in origin, and undoubtedly still evolving. There exists on the Presidentials an early stage in the evolution of a mountain Carabid fauna which requires, and is worth, careful analysis.

Presidential Carabidae are well known. The first list of "Mt. Washington" beetles, including 37 mountain Carabidae, appeared in 1874 (Austin); a more nearly complete list, in 1896 (Bowditch). In all, dozens of coleopterists have collected on the range. I have been there myself many times, at all seasons, collecting especially Carabidae, and in 1931 I compiled (as part of a doctoral thesis in the Department of Biology, Harvard University) a complete, annotated list of known New Hampshire Carabidae, covering lowlands as well as mountains, but with special attention to the Presidential Range. This list, corrected to 1940, is the source of present data.

The distribution of Carabidae in New Hampshire is complex, but for present purposes two main faunas may be recognized and contrasted: a *lowland fauna*, including all species found anywhere in the state below 2,000 ft. altitude, from the sea coast to the lower hills and valleys of the White Mts. region, and a *mountain fauna*, including all species found above 3,000 ft. on the Presidential Range. These arbitrary boundaries exclude the most confusing zone of transition, which lies near 2,000 ft. on

the lower mountain slopes. But even so, lowland and mountain faunas have some species in common.

Many winged, lowland insects, including many Carabidae, are carried up onto the Presidential Range by wind on flying days in early summer. Flights have often been observed, usually on the highest, exposed peaks, not on forested slopes. Bowditch (1896) says, "A warm day with a south wind produces a wonderful crop of beetles on the Summit [of Mt. Washington]; the air is filled with them; . . ."; and "a general list of Summit captures includes not only the strictly Arctic fauna, but very many chance visitors." These chance visitors actually include, among Carabidae, more species than are resident on the mountain! Many have been recorded at high altitudes only once or twice, and others are very erratic, common some years, apparently entirely absent others. They are not really mountain species. However, a few +winged Carabidae, common in open habitats in the lowlands, occur also commonly and regularly in open, exposed places above timber line on the Presidentials. There is no direct evidence as to whether or not these species are really resident above timber line, and they complicate the list of mountain species.

Many Carabidae have continuous ranges from the lowlands onto the forested mountain slopes of the Presidentials. A few other (Hudsonian) species have left populations more or less isolated in the upper mountain forest. But the *forest fauna* of the Presidentials is not really much isolated; the stranded or relict species in it are not sharply set apart. Above timber line, however, in the exposed Arctic-Alpine area, there are completely isolated populations of some true Arctic Carabidae. These are Arctic *relicts,* stranded since the retreat of Pleistocene ice.

In an appendix to this paper are listed all Carabidae definitely recorded from the Presidential Range above 3,000 ft. The —winged, ±winged, and +winged species are listed separately. Species recorded only once, twice, or erratically are indicated; they are +winged stragglers concerning which no further data are necessary. For other species, the following data are given, for reasons which will appear: whether geophiles or hydrophiles (no arboreal species is resident on the range); *if* hydrophiles, whether chiefly associated with swamps, wet ground, or streams (no species is specifically associated with open ponds); whether characteristic of forested zone, or of exposed area above timber line, or of both; and *if* of exposed area, whether Arctic relicts, or found also in open habitats in neighboring lowlands. The dimorphic species are individually discussed.

Carabidae recorded from the Presidential Range total 144 species. Of this number, 19, or 13%, are —winged; 3, or 2%, are ±winged *on the Presiden-*

Fig. 5. Presidential Range, White Mts., N. H.: aerial view of highest part, from the east, showing Pinkham Notch (2,032 ft.), forested slope, timber line (about 4,500 ft.), and exposed Arctic-Alpine area to summit of Mt. Washington (6,288 ft.). (Copyright C. T. Bodwell.)

tials; and 122, or 85%, are +winged. These figures may conveniently be summarized thus: 19—, 13%; 3±, 2%; 122+, 85%.

Of the total 144 species, 33 have been recorded from the Presidentials only once; 22, twice; and 24 others, erratically. These 79 species apparently reach the higher mountains only as +winged, flying stragglers. Without them, there are recorded from the Presidential Range 65 species, resident or of regular occurrence, with wings: 19—, 29%; 3±, 5%; 43+, 66%.

There remain on the Presidential list 18 +winged species which occur fairly regularly in the exposed Arctic-Alpine area above timber line, but which occur also, usually commonly, in open places in New Hampshire lowlands. There is no direct evidence as to whether these species are resident on the mountains or whether they are maintained by continual flights from below. But they are not Arctic species. None is listed from Labrador (Sherman 1910). Probably none really maintains a self-supporting population in the Arctic-Alpine climate on the Presidentials. If these species are removed, there remain on the Presidential list 47 resident Carabidae, with wings: 19—, 41%; 3±, 6%; 25+, 53%.

The resident Carabidae of the Presidential Range include 13 postglacial hydrophiles, species closely associated with swampy ponds and bogs which have followed glaciation. Most of these species occur impartially both above and below timber line, wherever they find suitable ponds and bogs. These species will all disappear as progress of erosion drains their habitats. All are +winged, like most hydrophiles. When they disappear, and if there is no other change in the mountain fauna, there will be left on the Presidential Range a residual fauna of 34 resident, permanent Carabidae, with wings: 19—, 56%; 3±, 9%; 12+, 35%.

The 34 species of this residual fauna are mostly geophiles, with a few hydrophiles which live beside small, rapid mountain brooks. Most of the species are characteristic either of forest below timber line or of the exposed area above; few are characteristic of both. The species are classified in various ways in Table 2.

In Table 3 are summarized (a) all native (American) Carabidae known from any part of the state of New Hampshire, including both lowlands and mountains; (b) all known from New Hampshire lowlands, below 2,000 ft.; and (c) all recorded from the Presidential Range, above 3,000 ft. And the table reviews (d-j) steps in analysis of the Presidential fauna.

Preceding comparisons and analysis have uncovered on the Presidential Range a resident, probably permanent, mountain Carabid fauna, with these characteristics: (1) It is a small fauna, consisting of few species, 24 in forest, 13 exposed. (2) Most of the species are geophiles; a few, brook-side hydrophiles; none, arboreal. (3) More than half of all species, and 64% to 70% of geophiles alone, are —winged.

TABLE 2. Classification of 34 species of Carabidae in the residual mountain fauna of the Presidential Range.

19 −winged: (geophiles)	12 forest, not or rarely exposed
	5 exposed, not or rarely forest (relicts)
	2 forest and exposed (1 relict, 1 not)
3 ± winged: (geophiles)	2 forest, not or rarely exposed
	1 exposed, rarely forest (relict)
12 +winged:	7 forest, not or rarely exposed
	4 geophiles
	3 hydrophiles (brooks)
	4 exposed, not or rarely forest
	3 geophiles (relicts)
	1 hydrophile (brooks) (relict)
	1 forest and exposed: hydrophile (brooks) (relict)
In forest:	14 −winged, all geophiles
	2 ± winged, both geophiles
	8 +winged: 4 geophiles
	4 hydrophiles (brooks)
Exposed:	7 −winged, all geophiles (6 relicts, 1 not)
	1 ± winged, geophile (relict)
	5 +winged: 3 geophiles (relicts)
	2 hydrophiles (brooks) (relicts)
Total, in forest, 24:	14−, 59%; 2±, 8%; 8+, 33%
Total, exposed, 13:	7−, 54%; 1±, 8%; 5+, 38%
Geophiles only, in forest, 20:	14−, 70%; 2±, 10%; 4+, 20%
Geophiles only, exposed, 11:	7−, 64%; 1±, 9%; 3+, 27%

TABLE 3. Summaries of Carabidae of New Hampshire and of the Presidential Range.

	Total species	− winged	± winged	+winged
a) All New Hampshire Carabidae.	298	40;13%	15; 5%	243;82%
b) Lowlands, below 2,000 ft.......	265	27;10%	14; 5%	224;85%
c) Presidentials, above 3,000 ft...	144	19;13%	3; 2%	122;85%
d) Presidentials, less stragglers....	65	19;29%	3; 5%	43;66%
e) Less probable non-residents....	47	19;41%	3; 6%	25;53%
f) Less post-glacial hydrophiles...	34	19;56%	3; 9%	12;35%
g) Residual forest fauna.........	24	14;59%	2; 8%	8;33%
h) Residual exposed fauna.......	13	7;54%	1; 8%	5;38%
i) Residual forest geophiles......	20	14;70%	2;10%	4;20%
j) Residual exposed geophiles....	11	7;64%	1; 9%	3;27%

Physical isolation, by impassable barriers, has played no part in the formation of this mountain fauna. The Presidential Range has been or is accessible to many Arctic, Hudsonian, and Canadian Zone Carabidae. Many species have reached the mountains. But few are established there.

Atrophy of wings has played no part in the formation of this mountain fauna. The distribution and relationships of the —winged species show as clearly as possible that all were —winged before they reached the mountains. So far as known, no dimorphic species has yet evolved a local, —winged mountain population (see discussion of ±winged species listed in Appendix).

Nevertheless, without isolation and without atrophy of wings, a mountain fauna has formed and is evolving on the Presidential Range. It has formed by *elimination* of a very large number of species, and by *concentration* of a few special species.

To find as accurately as possible how elimination has occurred, it is necessary to compare the mountain fauna in some detail with the surrounding lowland

fauna. Known lowland Carabidae of New Hampshire, below 2,000 ft., number 265 species, of which not quite 60% are geophiles, about 34% hydrophiles, and the balance arboreal. Table 4 gives a more detailed classification.

TABLE 4. Classification of lowland Carabidae of New Hampshire.

27	−winged, all geophiles		
14	±winged, all geophiles		
224	+winged, 115 geophiles		
	89 hydrophiles:	61 by ponds, swamps, etc.	
		24 by large streams	
		4 by small, rapid brooks	
	20 more or less arboreal		

Hydrophiles make up 1/3 of this lowland fauna, but, since there are no large streams on the mountain slopes and since ponds and swamps are disappearing, only the few hydrophiles (4 species) associated with small, rapid brooks can find counterparts in the final mountain fauna. Arboreal Carabidae, few in New Hampshire lowlands, are completely lacking in the mountain fauna. Geophiles make up the bulk of the lowland, as of the mountain, fauna, but are much more numerous in species in the lowlands, and differ in state of wings. In New Hampshire lowlands, geophiles number:

156 species: 27—, 17%; 14±, 9%; 115+, 74%

In the residual Presidential mountain fauna, in forest and exposed areas respectively, geophiles number:

20 species: 14—, 70%; 2±, 10%; 4+, 20%
11 species: 7—, 64%; 1±, 9%; 3+, 27%

These figures emphasize how few species even of geophiles belong to the mountain fauna. Even —winged species of geophiles are fewer in the mountains than in the lowlands, but the *proportion* of —winged species is far greater in the mountains, because the mountain fauna includes extraordinarily few +winged geophiles.

There exists, then, on the Presidential Range a mountain Carabid fauna, which has been formed not as a result of physical isolation and not by modification of species, but entirely by elimination and concentration of pre-existing species. Eliminated have been most (+winged) hydrophiles and all (+winged) arboreal species, and also a very large proportion of +winged geophiles. Concentrated have been chiefly —winged geophiles, with a very few +winged geophiles, and a few (+winged) brookside hydrophiles.

This Presidential mountain fauna is recent, post-Pleistocene, and still evolving. The mountain fauna is masked by many erratic and temporary species. Complicated analysis has been necessary to uncover it. But the fauna is not an analytical artifact. It is a true, typical mountain Carabid fauna, as will be seen below.

Note especially that —winged species are as numerous in forest as above timber line.

SOUTHERN APPALACHIAN MOUNTAINS

The southern Appalachian Mts., in southeastern United States, are more extensive and slightly higher than the White Mts. They are unglaciated, with a mature mountain topography of steep slopes and deep, narrow valleys, through which descend turbulent brooks. They lack ponds and swamps. They are heavily forested to their summits, except for an occasional, insignificant grassy or shrubby "bald."

The Appalachian Carabid fauna is not completely known, but it has been well sampled. Two samples will be considered here, one from Mt. Mitchell, 6,686 ft., in the Black Mts. of western North Carolina, the other from the Smoky Mts., 6,644 ft., on the North Carolina-Tennessee state line. Both samples were collected by myself in 1930. Each is the product of several days of intensive collecting, chiefly above 5,000 ft., but with some specimens taken down to about 3,000 ft. The two mountain samples are: Mt. Mitchell, 43 species: 25—, 58%; 18+, 42%; Smoky Mts., 41 species: 27—, 66%; 14+, 34%.

Lowland Carabidae of North Carolina probably (provisional manuscript list) number over 300 species, about 17% —winged.

The mountain samples, compared with the lowland fauna, show that the Appalachians do possess a mountain Carabid fauna with these characteristics: (1) It is a small fauna, with comparatively few species. (2) Most of the species are geophiles; a few, brook-side hydrophiles; probably none, arboreal. (3) More than half of all species, and a large majority of geophiles alone, are —winged.

This Appalachian mountain fauna is not physically isolated. Many lowland Carabidae could easily reach the mountains. But comparatively few have become established there.

The Appalachian mountain fauna has formed without, or with little, wing atrophy. The fauna is old, and many species are endemic, and it cannot be proven that none has lost its wings *in situ*, but most of the —winged species are derived from stocks which are —winged at low altitudes too.

The Appalachian mountain fauna has, in fact, as the ecology and relationships of the species show, been formed primarily by elimination and concentration. Eliminated have been most hydrophiles, probably all arboreal species, and very many +winged geophiles. Concentrated have been certain geophiles, chiefly —winged ones, and a few (+winged) brookside hydrophiles.

In some cases two or more localized mountain species appear to have evolved on the Appalachians from single —winged ancestors, by geographical differentiation or (slight) ecological radiation. This has considerably increased the number of —winged species in the Appalachian fauna as a whole, but has not greatly changed the ratio in samples from single localities.

There exists, then, on the southern Appalachians a mountain Carabid fauna which is older, purer, and more obvious than that of the Presidential Range,

but which is essentially similar, with the same three (numbered) characteristics, and which has been formed in the same way, primarily by elimination and concentration, but with some later multiplication of species in —winged stocks.

And this fauna is entirely sheltered in heavy mountain forest.

SANTA MARTA MOUNTAINS

The Sierra Nevada de Santa Marta, Colombia, northern South America, is a massif rising from sea level to 19,000 ft. Slopes are steep; valleys, deep, with many rapid brooks and mountain rivers, but without ponds or swamps except at very high altitudes, where retreating local glaciers have left numerous cold lakes (which, however, seem to have attracted no Carabidae). The slopes of the massif, at least on the west, are forested up to about 11,000 ft., thence exposed (grassy or rocky) to snow line.

During my residence south of Santa Marta, below these mountains, I twice ascended their western slope and spent in all about two days collecting in upper mountain forest (8,000 to 11,000 ft.) and above tree line (11,000 to 13,000 ft.), securing 15 species of Carabidae. They were: *in forest*, 7 species: 5 geophiles (all —winged), 1 brook-side hydrophile (+winged), 1 probably arboreal (+winged); *exposed*, 8 species: 6 geophiles (5—, 1 ±winged), 2 brook-side hydrophiles (both —winged).

Carabidae collected in lowlands south of Santa Marta, at the foot of these mountains, number 134 species, about ¼ geophiles, ½ hydrophiles, ¼ arboreal. Only 2 species are —winged, 132 +winged.

The mountain sample is probably incomplete, but it does show clearly the existence of a high-mountain Carabid fauna. (1) The fauna consists of few species. (2) Most of the species are geophiles; a few, brook-side hydrophiles; one, probably arboreal. (3) Practically all of the geophiles and also 2 hydrophiles are —winged.

Comparison with the adjacent lowland fauna suggests that the mountain fauna has been formed by elimination of large numbers of hydrophiles and arboreal species, and concentration of certain geophiles. But there are actually more different —winged stocks on the mountains than in the lowland fauna, which suggests that the wings of some species have atrophied in the mountain environment.

Note that mountain geophiles are —winged in forest as well as (usually) in exposed areas, but that the hydrophiles are —winged only when exposed.

MOUNTAINS OF THE GREATER ANTILLES

Several mountains of the Greater Antilles are comparable in height to the Presidential Range and southern Appalachians, but are more abrupt and isolated, rising from tropical lowlands near sea level. The mountains have a mature, unglaciated topography, and are forested. Antillean Carabidae, incidentally, have been the subjects of much of my collecting and study for a number of years.

Pico Turquino, Cuba (Figs. 6, 7), is the highest Cuban mountain, about 6,500 ft. Seven species of Carabidae have been found above 3,000 ft. on this mountain (Darlington 1937, pp. 117-8); 3 geophiles, 3 brook-side hydrophiles, 1 exclusively arboreal; all —winged. I collected on Turquino myself for two weeks in 1936 and secured 459 specimens of these 7 species, every specimen —winged. For comparison, lowland Carabidae of Cuba number 144, about 30% geophiles, 60% hydrophiles, 10% arboreal, with wings (*op. cit.*, p. 117, footnote): 1—, 1%; 4±, 3%; 139+, 96%. The 7 Turquino species belong to 5 stocks: *Ardistomus, Bembidion*, 2 groups of *Colpodes*, and *Phloeoxena*. The *Bembidion, Phloeoxena*, and 1 group of *Colpodes* have +winged relatives at lower altitudes in Cuba, and have probably undergone wing atrophy *in situ* on Turquino. The phylogenies of the *Ardistomus* and of the other group of *Colpodes* are doubtful.

The Blue Mts., Jamaica, rise to 7,388 ft. Carabidae (Darlington 1941) are incompletely known on the lower slopes, but above 5,000 ft. are 10 species; 8 geophiles, 0 hydrophiles (I found no streams above 5,000 ft. in the Blue Mts.), 2 probably arboreal; with wings: 8—, 80%; 2+, 20%. The geophiles are all —winged; arboreal species, +winged. For comparison, lowland Carabidae of Jamaica number 63, about 30% geophiles, 60% hydrophiles, 10% arboreal, and are all +winged. The 8 —winged Blue Mts. species belong to 5 independent genera: *Pachyteles, Tachys, Morion, Colpodes*, and *Apenes*. Of the first 3 of these genera, no —winged species are known anywhere else in the Antilles; the Blue Mts. species have almost certainly undergone wing atrophy *in situ*. The *Apenes*, too, appears to have evolved locally from a +winged ancestor. The phylogenies of the *Colpodes* are unknown.

Mountains of Hispaniola include three high massifs: La Selle (about 9,000 ft.) and La Hotte (7,800) in Haiti, and the Cordillera Central (10,000) in the Dominican Republic. Each has an endemic mountain Carabid fauna of 6 to 15 species in single localities. Geophiles predominate, with fewer brook-side hydrophiles and arboreal species. Geophiles are almost all —winged; hydrophiles and arboreal species, usually +winged, occasionally —winged. For comparison, known lowland Carabidae of Hispaniola number 97, with hydrophiles probably in majority, and almost all species are +winged. On each massif, one or more —winged species appears, from its relationships, to have lost its wings *in situ*, but the phylogenies of many species, especially of Colpodes, are doubtful.

Greater Antillean mountains less than 5,000 ft. high sometimes possess a few —winged Carabidae, but the species are usually derived from —winged stocks of other, higher mountains. *E.g.*, the mountains of Puerto Rico (4,000 ft.) have 3 —winged stocks, all probably derived from the high Cordillera Central of Hispaniola (Darlington 1939, pp. 79-80). Carabid wings seem rarely to atrophy below 5,000 ft. on the Greater Antilles, and on mountains of less

FIG. 6. Pico Turquino, Cuba: aerial view of upper 2/3 of south slope. (Photo by Stephen Taber.)

than 3,000 ft. —winged Carabidae are usually absent.

To sum up: Greater Antillean mountains over 5,000 ft. high all possess mountain Carabid faunas like those of continental mountains: (1) small faunas; (2) varying in composition but usually composed chiefly of geophiles, with fewer (or no) brookside hydrophiles and arboreal species; and (3) with most geophiles and even sometimes hydrophiles and arboreal species —winged. These faunas have evolved partly by concentration (of certain geophiles) and elimination (especially of hydrophiles). But Carabidae are rarely —winged in Antillean lowlands. The —winged mountain species cannot be concentrated lowland forms, and their distribution and relationships show that many of them have in fact evolved locally, on different mountains, by *conversion, i.e.*, by atrophy of wings of +winged ancestors. Conversion has been followed in some cases, especially in *Colpodes*, by a certain amount of geographical differentiation and radiation, which have slightly increased the number of species on some mountains. And —winged groups which have been converted on higher mountains have occasionally invaded mountains of less than 5,000 ft.

All —winged Carabid stocks of Greater Antillean mountains are characteristic of, and usually confined to, dense cloud-forest (Fig. 7).

VII. MOUNTAIN FAUNAS: DISCUSSION

The characteristics of mountain Carabid faunas are: (1) They are small faunas, of relatively few species. (2) Most of the species are geophiles, but each mountain fauna usually includes a few brookside hydrophiles and sometimes, in the tropics, one or more arboreal species. (3) Most of the geophiles, and sometimes the hydrophiles and arboreal species too, are —winged, as a result either of concentration of pre-existing —winged stocks or of conversion of +winged stocks. In either case, number of —winged species may be increased in old faunas by geographical differentiation or by radiation. Faunas with these three characteristics occur on diverse mountains: temperate and tropical, continental and insular, exposed and forested. There must be strong forces acting on mountains to produce such faunas. What are the forces?

First to be considered are certain relatively simple factors which might directly affect the wings and flight of mountain Carabidae.

Altitude above sea level might affect wings and flight. Low atmospheric pressure at high altitudes might conceivably inhibit development of wings, and rarity of air might make flight mechanically difficult. Whether or not altitude does have an effect should be shown by comparison of the Carabidae of Colo-

FIG. 7. Pico Turquino, Cuba: cloud forest on summit, across small artificial clearing. (Photo by P. J. Darlington, Jr., June, 1936.)

rado with those of New Hampshire. Colorado is high. The lowest point in the state is 3,386 ft. above sea level, and the plains of eastern Colorado rise gradually to about 6,000 ft., to the foot of the Rocky Mts. Carabidae in lowland habitats in Colorado live 3,500 or 4,000 ft. higher than Carabidae in corresponding habitats in New Hampshire. In fact the lowland Carabidae of Colorado live at almost exactly the same altitude as the mountain Carabidae of the Presidential Range. The Carabid faunas of Colorado* and of New Hampshire compare thus: Colorado, 305 species; wings: 46—, 15%; 10±, 3%; 249+, 82%. New Hampshire, 298 species; wings: 40—, 13%; 15±, 5%; 243+, 82%. Obviously, the Colorado fauna has none of the characteristics of a mountain fauna. Mountain faunas consist of few species, but Colorado possesses about the same number as New Hampshire, and the proportion of —winged species is not significantly different. This is a fair comparison. The Carabid fauna of Colorado is similar to that of New Hampshire in every way, composed of many lowland and fewer mountain species, derived chiefly from the same or similar genera, and similar in ecological composition, except that geophiles in Colorado are often xerophiles rather than mesophiles. The comparison shows as conclusively as possible that a difference in altitude above sea level of 3,500 or 4,000 ft. has, of itself, no important effect on Carabid faunas.

Exposure to wind (Darwin's factor) and *straggling* may possibly remove +winged flying Carabidae, and result in selection of —winged flightless forms, in special cases, but can hardly be of general importance. If wind and straggling have any effect at all, it should be greatest in exposed places. On the Presidential Range, however, the proportion of —winged species is as great in sheltered forest as in exposed areas above timber line; on the Santa Marta Mts., *geophiles* are —winged below as well as above timber line; and high proportions of —winged species occur on other mountains which are entirely covered by dense, non-deciduous forest. (Dense forest itself does not induce wing atrophy, for in some dense lowland forest, *e.g.* at Barro Colorado, Panama, all known Carabidae are +winged.) Among geophiles, then, there is no indication whatever that —wingedness of mountain species is correlated with exposure. Some correlation may occur among hydrophiles, which, on the Santa Marta Mts., are —winged only above timber line. But some brook-side hydrophiles of Antillean mountains are —winged in forest.

As for *temperature*, mountains are always cooler than surrounding lowlands and are sometimes very cold, and cold might conceivably either inhibit development of wings or restrict flight. Actually, cold seems not to inhibit wing development. Some Carabidae are +winged in the Arctic, in very cold places. Existence of dimorphic species indicates that wing atrophy of Carabidae is primarily genetic, not physiological. And on some cold mountains (Presidential Range) —winged species are all pre-existing forms, concentrated, with no suppression of wings by cold or any other factor.

There is, however, some correlation between temperature and wing-state of Carabidae. In hot American tropics, most species are +winged; in cool temperate regions, many are —winged. This may be due partly to an effect of temperature on flight (but see p. 41, and Fig. 4). Flight requires great physiological activity. Heat favors it. Insects in warm regions can fly easily and often. Cold hinders flight and may limit it to certain seasons and certain times of day. Cold does not make flight harmful, but does reduce its ease and usefulness, and may thus tend to throw the selective balance toward flightlessness. Cold may thus indirectly favor flightless, —winged Carabidae on mountains. But effect of cold on lowland Carabidae is not profound; +winged species are in majority even in very cold places, *e.g.* in Labrador. The effect of cold as an independent factor can hardly be more profound among mountain species, especially not on mountains so warm as those of the Greater Antilles.

* From Wickham's (1902) list of Colorado Coleoptera, with a few corrections and additions. Wings have been examined in many Colorado specimens in the Museum of Comparative Zoölogy. Species counted as dimorphic are known to be so in some parts of their ranges, but dimorphism has not yet been demonstrated for all of them in Colorado populations.

Finally, *freedom from flooding* may have a slight effect. Lowland Carabidae, even geophiles, often fly to escape from standing flood water. Floods cannot stand on mountain slopes, and mountain Carabidae do not need to fly to escape from them, and this may slightly reduce usefulness of flight and shift the selective balance a little toward flightlessness among mountain species, but it can hardly be important.

Apparently the —wingedness of mountain Carabidae is not due primarily to any of these simple factors, although coolness may be of some indirect importance. The characteristics of mountain Carabid faunas are really rather complex (—wingedness is only one of them), and it seems likely that the faunas evolve for complex reasons.

Mountains are small areas of land considerably and rather abruptly elevated above their surroundings, and they usually have a special topography and special climate. Factors inherent in the nature of mountains as thus defined are: *Limitation of habitats:* mature mountains lack all habitats which go with standing and slowly flowing water, with large rivers, broad valleys, and level plains, and probably lack other, less obvious special niches. *Limitation of area:* mountains are *small* elevated areas, climatically differentiated and ecologically isolated. *Habitability and stability of environment:* mountains which rise more than 3,000 or 4,000 ft. often, especially in the tropics, enter a cloud zone where regular precipitation maintains dense, damp cloud-forest or damp Alpine areas, where Carabidae thrive. And these favorable habitats tend to be stable, not only because rainfall is regular, but because broad fluctuations of climate, which shift life zones hundreds or thousands of miles north or south at low altitudes, shift them only a few hundred or thousand feet up or down mountain slopes, forcing faunas to move only a little. Other factors are *coolness,* which may be indirectly important (see above), and *freedom from flooding* and perhaps sometimes *exposure to wind,* which are probably of minor importance.

These factors, by their effect on evolution of Carabid faunas and of Carabidae, appear to be responsible for the three observed characteristics of mountain Carabid faunas, thus:

1. Mountain Carabid faunas consist of few species. Accounted for by limitation of habitats, which excludes many species especially of hydrophiles from mountain faunas, and by limitation of area, which limits number of species in remaining habitats. The profound effect of limitation of area in limiting number of species has been discussed in Section III. Note: temperature is probably not a limiting factor so far as number of species goes except perhaps on very cold mountains, for Carabidae are abundant in cool-temperate climates.

2. Mountain Carabid faunas consist chiefly of geophiles, with usually a few brook-side hydrophiles and sometimes a few arboreal species. Accounted for primarily by limitation of habitats, which excludes hydrophiles except brook-side species, and excludes also arboreal species at least on open mountains, leaving mostly geophiles. But other factors are probably involved in minor ways. *E.g.,* limitation of *area* may tend to exclude arboreal Carabidae even on forested mountains if, as is likely, arboreal species usually maintain sparse, unstable populations not adapted to existence in small areas. Since geophiles probably more often than other Carabidae maintain dense, stable populations, incapable of flight, any factors which favor such populations, or which diminish need of flight, indirectly favor concentration of geophiles.

3. In mountain Carabid faunas, a majority of species, including most of the geophiles and sometimes hydrophiles and arboreal species too, are —winged, as a result either of concentration of pre-existing —winged forms or of conversion of +winged forms. Accounted for as follows:

In concentration: limitation of habitats, plus minor factors, eliminates most hydrophiles and arboreal species, which are usually +winged, and concentrates geophiles, which are often —winged. Among geophiles, further elimination of +winged and concentration of —winged species may occur to an extent suggested by comparison of the geophiles of New Hampshire lowlands (27—, 14±, 115 +winged) with those of the residual mountain fauna of the Presidential Range (19—, 3±, 7 +winged). In accounting for concentration of —winged species among geophiles one must distinguish between the factor which impels concentration and the factors which determine its direction. The impelling force apparently comes from limitation of area, which limits number of species even of geophiles on mountains and necessitates severe elimination and selection. But that *—winged* geophiles are selected probably depends on several factors. Limitation of area itself favors those species, probably often —winged, which maintain dense, stable populations (see end Section IV). Habitability and stability of environment, coolness, and freedom from flooding reduce the usefulness of flight and help to uncover a selective advantage probably inherent in —wingedness (see Section V, and below). And exposure to wind and straggling of +winged flying forms may add something (apparently not much) to the advantage of —winged species. Note that concentration of —winged species on mountains can occur as a rule only among geophiles and only in temperate or cold parts of the world, *i.e.,* only in that ecological group and in those climatic zones where —winged species are numerous in lowland faunas. Among hydrophiles and arboreal species, and geophiles too in the tropics, —winged species on mountains must usually be products of local conversion.

In conversion: it has been found (Section V) that many factors combine in complex ways to determine whether flight is useful to Carabidae and whether +wings are retained or lost. Among lowland Carabidae, the balance of factors is such that flight is useful and +wings retained in a majority of species, but the balance is often close and can be reversed by change in any of several factors. On mountains,

several factors probably combine to reverse the balance strongly toward —wingedness. Among lowland Carabidae, flight serves to maintain sparse, unstable populations in large, unstable areas. This seems to be the principal function of flight among lowland geophiles, and an important function among hydrophiles and arboreal species too. On mountains, limitation of area, resultant density and stability of populations, and habitability and stability of environment probably make flight unnecessary to maintain populations, so that flight loses its most important function, and coolness and freedom from flooding may further limit usefulness of flight. It is likely that most mountain geophiles find flight useless, but not necessarily harmful, and that their wings atrophy by selection of —winged mutants which owe their selective advantage to inherent simplicity and vitality, not to flightlessness. This is probably the principal active or impelling process in conversion of wings of mountain geophiles. Exposure and straggling of flying individuals seem not to be concerned in conversion of geophiles but may be more important among hydrophiles and arboreal species, which fly more actively and are therefore more likely to straggle, and which do sometimes become —winged on mountains. Among hydrophiles, at least, —wingedness is sometimes correlated with exposure (on Santa Marta Mts.). Conversion of wings of all sorts of Carabidae may be helped along a little by nonselective genetic processes (recurrent mutation and secondary effects of evolution of organs other than wings), but these processes are presumably no more rapid on mountains than in other places, and are probably less important in conversion than in later stages of wing atrophy.

Concentration (of —winged species) and conversion have much in common. Both are selective. In concentration, excessive numbers of species have access to a mountain fauna, and selection of —winged species occurs. In conversion, excessive numbers of individuals are produced in successive generations in mountain populations, and selection of —winged

<table>
<tr><th>Limitation of habitats</th><th>Limitation of area, and resultant density & stability of populations</th><th>Habitability & stability of environment
Coolness
Freedom from flooding</th><th>Inherent superiority of -winged forms</th><th>Exposure, straggling of +winged forms</th><th>Non-selective genetic processes</th><th>Geographical differentiation, & radiation</th></tr>
<tr><td colspan="2">Factors limiting number of species</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Main factor concentrating geophiles</td><td colspan="4">Other factors perhaps contributing indirectly to concentration of geophiles</td><td></td><td></td></tr>
<tr><td></td><td>Main factor impelling concentration among geophiles</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td colspan="4">Factors directing concentration of -winged species among geophiles</td><td></td><td></td></tr>
<tr><td></td><td colspan="2">Factors permitting conversion by reducing usefulness of flight</td><td></td><td colspan="2"></td><td></td></tr>
<tr><td></td><td></td><td></td><td>Main factor impelling conversion</td><td colspan="2">Minor processes aiding conversion</td><td></td></tr>
<tr><td></td><td></td><td></td><td></td><td></td><td></td><td>Processes increasing proportion -w. species</td></tr>
</table>

TABLE 5. Principal factors and processes apparently concerned in formation and evolution of mountain Carabid faunas.

individuals occurs (this is simple natural selection, of course). And factors modifying the two processes are much the same. Those factors which favor —winged species usually favor —winged individuals too.

Both concentration and conversion may be followed, in habitable, stable mountain environments, by geographical differentiation and radiation of species in —winged stocks, but these processes are usually not extensive on mountains which, like those discussed above, derive their faunas from diverse lowland faunas.

Table 5 summarizes the principal factors and processes which appear to be concerned in formation and evolution of mountain Carabid faunas.

By way of clarification, co-ordination, and elaboration of parts of the preceding discussion, suppose that, in the midst of lowlands stocked with diverse Carabidae, a small area of land gradually rises to form a mountain, and the mountain then gradually expands to form a high plain. Three stages in evolution of the mountain Carabid fauna are to be expected during this hypothetical cycle.

The first stage is one of increasing concentration. From the beginning, as a limited area of land is elevated, there occurs elimination of hydrophiles associated with large rivers and standing water. Elimination and concentration of different Carabidae continue as the mountain becomes higher, as mountain topography develops, and as ecological differentiation and isolation increase, until a true mountain fauna is formed, of few species, chiefly geophiles, and chiefly —winged, if —winged species are available.

The second stage is that of maximum definition. The fauna is fully concentrated and conversion may occur. The presence of pre-existing —winged species probably tends to prevent establishment and conversion of +winged species in the same habitats. In the absence of prior —winged forms, conversion is extensive among geophiles and occasional among hydrophiles and arboreal species. Conversion seems to take place mostly on mountains which exceed a certain critical altitude above surrounding lowlands and which have a certain area above that altitude, sufficient for establishment and isolation of populations of +winged Carabidae. On Antillean mountains, where conversion has occurred chiefly on mountains which rise 5,000 ft. or more, the critical altitude is probably about 3,000 ft. (where cloud-forest often begins) and area above that altitude is of the order of a very few square miles. Under these conditions, every +winged Carabid in a mountain fauna may be converted, probably chiefly by selection of inherently superior —winged mutants in an environment where flight is useless.

The third stage in the hypothetical cycle is that of decreasing definition. As the mountain expands to form a high plain, area increases and habitats become more diverse, forces of concentration decrease, flight becomes useful again to many Carabidae and conversion is inhibited, and the Carabid fauna gradually reverts to a fauna of lowland type (*cf.* fauna of Colorado plains, p. 51), if a proper variety of lowlands species can reach the high plain.

VIII. ISLAND FAUNAS: DATA

Below are summarized the approximate position, area, altitude, and nature of a variety of islands, near to continents and remote, small and large, low and high, temperate and tropical, together with what is known of the Carabid fauna of each.

Islands Near Continents, with Non-endemic Faunas: Mount Desert Island, Nantucket, Santa Barbara Islands, Pribilof Islands, and Iceland

Mount Desert Island: recent continental island separated from coast of Maine, northeastern United States, by channel a few hundred feet wide; 100 sq. mi.; 1,500 ft.; rugged; ecologically diverse, with forest, open country, and much postglacial fresh water, but no *large* streams. Known native Carabidae (listed by Procter 1938): 97 species, all identical with mainland species; just over 2/3 geophiles, about 1/4 hydrophiles, few arboreal; wings of island specimens not examined, but presumably same as in mainland populations of same species: 14—, 15%; 8±, 8%; 75+, 77%. These figures are intended to show merely what proportion of the mainland fauna occurs on Mount Desert. The island fauna is not much modified, but does include fewer species, with slightly greater proportions of geophiles and of —winged forms, than expected on an equal mainland area. These differences are due partly to absence from Mount Desert Island of some +winged hydrophiles associated with large streams.

Nantucket Island: recent continental island 28 miles south of Cape Cod, Massachusetts, northeastern United States; 47 sq. mi.; 91 ft.; flat, open but probably once forested, much burned. Known native Carabidae (Johnson 1930): 76, all identical with mainland species; ecological composition of fauna nearly as on adjacent continent, but with a few less hydrophiles and more arboreal species than expected; wings, again assumed to be same as in mainland specimens of same species: 5—, 7%; 5±, 7%; 66+, 86%. This island fauna is perhaps incompletely known, but it appears to include fewer species than occur in similar areas on mainland, and significantly *fewer* —winged stocks. Explanation is doubtful. Part of original Carabid fauna may have been destroyed by clearing and burning and replaced by +winged immigrants. Or a +winged fauna may be evolving naturally on this low island.

Santa Barbara Islands: rather recent continental islands 20 to 65 miles off coast of southern California, western United States; 8 islands, largest about 100 sq. mi.; 2,400 ft.; rugged; warm temperate, rather dry. Carabidae: 40 species listed (Fall 1897), most identical with mainland species; majority geophiles, some hydrophiles, none arboreal; wings, assumed to be same as in mainland specimens of same

species: probably 6—, 34+. Carabidae later listed from the largest island, Santa Cruz, alone (Fall and Davis 1934): 15 species; wings: 2—, 13+. In this case I have examined island specimens of 9 of the species. Wings are the same as in mainland specimens in each case. No exact comparative data are available, but proportion of —winged species is probably less on the islands than on the Californian mainland.

Pribilof Islands: volcanic islands in Bering Sea 200 miles off Alaska; largest island 35 sq. mi.; 600 ft.; rugged; mild Arctic climate, vegetation low. Carabidae (Van Dyke 1921, Wickham 1923, with corrections): at least 12 species, identical or nearly so with mainland species; most geophiles, 2 or 3 hydrophiles; wings: probably 7—, 5+. No exact comparative data are available, but proportion of —winged species is certainly greater on the islands than on the Alaskan mainland.

Iceland: volcanic island about 200 mi. east of Greenland, farther west of Europe; 40,000 sq. mi.; 6,250 ft., but habitable only at low altitudes; rugged, locally glaciated; climate mild-Arctic, vegetation chiefly Arctic European. Established Carabidae (Lindroth 1931): 18, all identical or nearly so with European or circumpolar species; majority probably geophiles, but some hydrophiles. State of wings unknown for species in Iceland, but in European populations of same species wings are 2—, 11%; 6±, 33%; 10+, 56%. Strict —winged stocks are surprisingly few; dimorphic stocks, numerous; it would be interesting to know in what direction the dimorphic species* have evolved on Iceland.

REMOTE ISLANDS: MADEIRA, ST. HELENA, HAWAIIAN ISLANDS, SEYCHELLES, AND BERMUDA

Madeira: volcanic, probably oceanic island in Atlantic Ocean 350 mi. off NW. coast of Africa; about 300 sq. mi.; 6,000 ft.; mountainous; climate mild, habitats fairly diverse. Carabidae (listed by Jansson 1940): 92 species, many endemic; majority geophiles, some hydrophiles, a few arboreal (Wollaston 1854); wings (Wollaston; Jeannel 1938); nearly 2/3 of species —winged, 1/3 or more +winged, state of wings of a few unknown. Fauna is of Mediterranean origin, modified on Madeira by evolution of endemic species and genera. Fauna is diverse; no one group dominates it; —winged species are in some 17 independent genera; but species have multiplied a little locally in certain genera. Some stocks may have reached Madeira —winged, *e.g. Trechus* (Jeannel 1925) and perhaps some *Pterostichini,* but other —winged stocks appear to have been converted on Madeira from +winged ancestors. The —winged forms are numerous in wet mountain forest as well as in exposed places.

St. Helena: volcanic, oceanic island in remote South Atlantic Ocean, 1,200 mi. from nearest continent (Africa); 47 sq. mi.; 2,700 ft.; rugged; mild, originally with much wet forest. Carabidae (Wollaston 1877): 14 species; 13 geophiles, 1 hydrophile (the +winged *Bembidion*). The species are: *Haplothorax burchelli* Waterh. (endemic genus) —w; *Calosoma maderae helenae* (endemic subspecies) +w; *Bembidion,* 12 species: 1 (endemic species) +w.; 11 (endemic subgenera) —w. (also, *Laemostenus complanatus,* introduced). Wings of native species: 12—, 86%; 2+, 14%. The native species may all be derived from 3 immigrants, which *may* all have been +winged when they reached Madeira. There has certainly been extensive radiation in *Bembidion.* The —winged *Bembidion* all live sheltered in damp forest on the highest ridge of the island.

Hawaiian Islands: volcanic, oceanic islands in remote Pacific Ocean, about 2,000 mi. from nearest continent (North America); largest island (Hawaii) about 4,000 sq. mi.; 13,825 ft.; mountainous; subtropical, ecologically diverse, formerly much wet forest as well as drier, more open country. Carabidae (Sharp 1903, esp. pp. 178, 187, 289, etc.): 204 species, but no more than 80 on a single island; majority apparently geophiles, very few hydrophiles, but numerous arboreal species; wings (according to Sharp): 184—, 90%; 20+, 10%. Sharp did not at this time recognize wing dimorphism in Carabidae. At least one and perhaps more Hawaiian species are really ±winged. Of the few additions made to the Hawaiian Carabid list since Sharp, the most important is a minute (0.8 mm.), blind, —winged, apparently endemic genus of *Anillini* (Jeannel 1937, pp. 323-5), a tribe which is entirely blind and —winged. This Hawaiian Carabid fauna is almost wholly endemic, derived almost entirely from 3 old stocks, each of which has radiated enormously. Two of the stocks *(Bembidii, Agoni)* still include a few +winged among many —winged Hawaiian species; the third stock *(Cyclothoraces)* is now entirely —winged on Hawaiian Islands, but +winged relatives occur in Australia; probably all 3 stocks were +winged when they reached Hawaii. Many —winged Hawaiian Carabidae inhabit wet forest rather than exposed places; in fact a good many —winged species, in several genera, are arboreal!

Seychelles Islands: islands of doubtful origin in Indian Ocean 600 mi. NE. of Madagascar, much farther SW. of India; largest island (Mahé) 55 sq. mi.; 3,000 ft.; rugged; mild tropical, formerly much wet forest. Carabidae (Scott 1912, pp. 243-252; 1933, pp. 342, 357): 8 species seen by Scott (a few more recorded); all from cultivated lower country, "endemic forests appear to be devoid of Carabidae"; wings: 1—, 12%; 1±, 12%; 6+, 76%. The —winged species is another minute (1.5 mm.), blind, probably endemic genus in the blind, —winged tribe *Anillini.* Only 1 or 2 other Seychelles Carabidae are endemic; the rest, wide ranging. This Carabid fauna is recent, little differentiated, and the island habitat seems not to have modified the wings of any species. Yet the Seychelles possess remarkable endemic Amphibia, and must be old, stable, habitable islands, once more accessible than now.

* *Notiophilus aquaticus* and *N. biguttatus, Bembidion grapei, Trechus obtusus, Calathus melanocephalus, Pterostichus diligens.*

Bermuda: an island with volcanic, oceanic base, in Atlantic Ocean 575 mi. from North America; 19 sq. mi.; 260 ft. (in past, much larger and higher); subtropical, vegetation light, no true forest. Carabidae (Ogilvie 1928, p. 11, and material in Museum of Comparative Zoölogy): 5 species;* 4 geophiles (1 or 2 of which are facultative hydrophiles), 1 arboreal; wings: all +winged. *Laemostenus complanatus* is introduced, probably from Europe; the other species are identical or nearly so with species of eastern United States. Bermudan Carabidae are thus few, all +winged, scarcely differentiated, although Bermuda is biologically a fairly old island, with endemic land snails and an endemic lizard.

West Indian Islands

The West Indies lie in and around the Caribbean Sea between North and South America. They include:

Greater Antilles: old islands of complex origin; 40,000 (Cuba) to 3,400 sq. mi. (Puerto Rico); 10,000 (Hispaniola) to 4,000 ft. (Puerto Rico); each island with lowlands and local or extensive mountains; mild tropical, each island ecologically diverse. Carabidae less numerous than in equal areas on continent, varying in number with area of islands (Table 1). Lowland species (of Cuba, Jamaica) are more than 30% geophiles, nearly 60% hydrophiles, hardly 10% arboreal. Lowland species are almost all +winged; *e.g.*, in Cuban lowlands (Darlington 1937, p. 117) are 144 species, with wings: 1—, 1%; 4±, 3%; 139+, 96%. In Jamaican lowlands (Darlington 1941) are 63 species: all +winged. The Greater Antillean fauna is fairly old, with numerous endemic species even in lowlands.

Lesser Antilles: rather diverse islands of doubtful history; each a few hundred sq. mi. or less; 3,000 to 5,000 ft. Carabidae (incompletely known): 39 species examined from various islands; probably 23 geophiles, 14 hydrophiles, 2 arboreal; wings: 3—; 36+. The —winged species are from mountainous localities. Lowland species are all +winged. Fauna is fairly old, with some endemics.

Low West Indian Islands include *Bahamas:* 1,600 sq. mi. (Andros) to minute cays; greatest altitude 400 ft. (Cat Is.); flat, rather dry, no real forest. Bahaman Carabidae (incompletely known): 19 species examined; probably 10 geophiles, 8 hydrophiles, 1 arboreal; wings: all +winged. *Cayman Islands, Swan Island,* and *Navassa,* all small and low, also are known to possess some Carabidae: all +winged. Faunas of all of these low islands, including Bahamas, are recent, with practically no endemism.

Practically all Carabidae which have reached the West Indies (chiefly from Central America, some from Florida, a few from elsewhere) appear to have arrived and dispersed as +winged, flying forms; —winged stocks which have originated on West Indian mountains have not spread far, and several —winged stocks (*Pasimachus, Dicaelus,* some *Pterostichini*) which flourish on the peninsula of Florida are absent from the West Indies.

* *Agonum cinticolle. Agonum* (near) *punctiforme, Agonoderus lineola, Lebia viridis, Laemostenus complanatus.*

IX. ISLAND FAUNAS: DISCUSSION

Carabid faunas of islands have some of the characteristics of mountain faunas, but are more variable. Different sorts of islands have different sorts of faunas, and some old and habitable islands have practically no endemic faunas at all (Seychelles, Bermuda). Much more information is needed about the Carabidae of different islands. But the following generalizations seem justified now.

1. Island Carabid faunas, like mountain faunas, are small, with fewer species than occur in equal areas on continents, and, other things being equal, number of species varies with size of islands. This has been shown (Section III) probably to be an effect primarily of limitation of area, supplemented by limitation of habitats. But on old, mountainous islands (Madeira, Hawaiian Islands) Carabidae tend to evolve increasing numbers of very local, usually —winged endemic species.

2. Island Carabid faunas vary in ecological composition, but, like mountain faunas, usually include relatively more geophiles, and fewer hydrophiles and arboreal species, than do continental faunas. A trend in this direction appears even on the Greater Antilles, as compared with continental tropical America, and the trend is stronger on smaller islands, where geophiles seem always to be in considerable majority. This is accounted for in part by limitation of habitats. Lack of habitats excludes at least river hydrophiles from small islands. But limitation of area may be more important: geophiles probably more often than hydrophiles or arboreal Carabidae maintain dense, stable populations fit to exist on small islands.

3. Island Carabid faunas vary in state of wings. On *mountainous islands* which are habitable and more than 5,000 ft. high (Madeira, Hawaiian Islands), most Carabidae are —winged. On such islands everywhere —winged faunas probably evolve in much the same way and for the same reasons as on mountains on continents. On mountainous islands which are continental in origin, formed by subsidence of continental areas, island faunas may be the original, persistent mountain faunas, and —winged species may simply be concentrated. On mountainous islands which are oceanic, reached chiefly by +winged Carabidae, conversion becomes of first importance. And if the islands are very remote, reached by few Carabidae of any sort (St. Helena, Hawaiian Islands), conversion may be followed by very extensive radiation and multiplication of —winged species. On *intermediate islands,* flat or rugged but not mountainous, and not tropical, wings of Carabidae are extremely variable. On *low, tropical islands* (low West Indies) most Carabidae are +winged.

These facts show that mere existence upon an island, independent of other factors, has no uniform

nor profound effect on Carabid wings, and it follows, I think, that exposure to wind, and straggling of +winged flying forms, are not more important factors on islands than they have been found to be on mountains. State of wings of Carabidae on islands is correlated not with exposure, but, on the one hand, with mountainousness, and on the other, with tropical climate. The contrast, in the West Indies, between mountain faunas, —winged even in sheltering forest, and lowland faunas, +winged on islands of every size, even on small islands exposed to trade and hurricane winds, is particularly striking and significant. The explanation probably is that, while flight is of little use to most Carabidae on mountains and on mountainous islands, it is useful on low tropical islands. On mountains, limitation of area, resultant density and stability of populations, and habitability and stability of environment tend to make flight unnecessary to maintain populations, and coolness and freedom from flooding further limit usefulness of flight. On low islands, area is usually not so limited as on mountain tops (Carabidae may not be able to maintain themselves on very small low islands, which, in the West Indies, usually lack endemic species) and environment is not so habitable (often drier) nor so stable (liable to submergence and climatic change), and Carabid populations are probably therefore more sparse, unstable, and more often maintained by flight. And low islands in the tropics are warm, so that Carabidae can fly easily and often, and flat islands are liable to flooding, which increases usefulness of flight.

In last analysis, the different wing-states of Carabidae on mountains and on low tropical islands are seen to be due not to impelling forces, which are more or less constant, but to different modifying factors. On low tropical islands, as on mountains, limitation of area limits number of species and impels concentration, but modifying factors are such that flight is useful on the islands, and +winged, not —winged, species are concentrated, as they have been not only on the West Indies but perhaps even on Nantucket, which is not tropical. And on low tropical islands, as on mountains, —winged mutants presumably appear which are inherently superior except that they cannot fly, but they are suppressed and conversion is inhibited by selection of flying individuals. All this is diagrammed in Figure 8.

SUMMARY AND CONCLUSIONS

Section I. Carabidae are cosmopolitan, numerous, usually predaceous beetles. Some are geophiles (simply ground-living); some, hydrophiles (associated with open water); some, arboreal. Most are +winged (fully winged) and usually can fly, but 1/5 or 1/4 of all species are —winged (wings reduced or vestigial) and flightless, and a few are ±winged (dimorphic). The —winged and ±winged species are mostly geophiles, rarely hydrophiles or arboreal.

II. Continental Carabid faunas vary in number of species, in ecological composition, and in state of wings. Temperate faunas consist of many species; many geophiles, fair numbers of hydrophiles, few arboreal; and some or many geophiles are —winged. Tropical faunas (in America) consist of relatively fewer species; fewer geophiles, more hydrophiles, fair numbers arboreal; and practically all species are +winged.

III. Limitation of area is found to limit number of species of Carabidae which occur together in isolated places (on islands of the Greater Antilles).

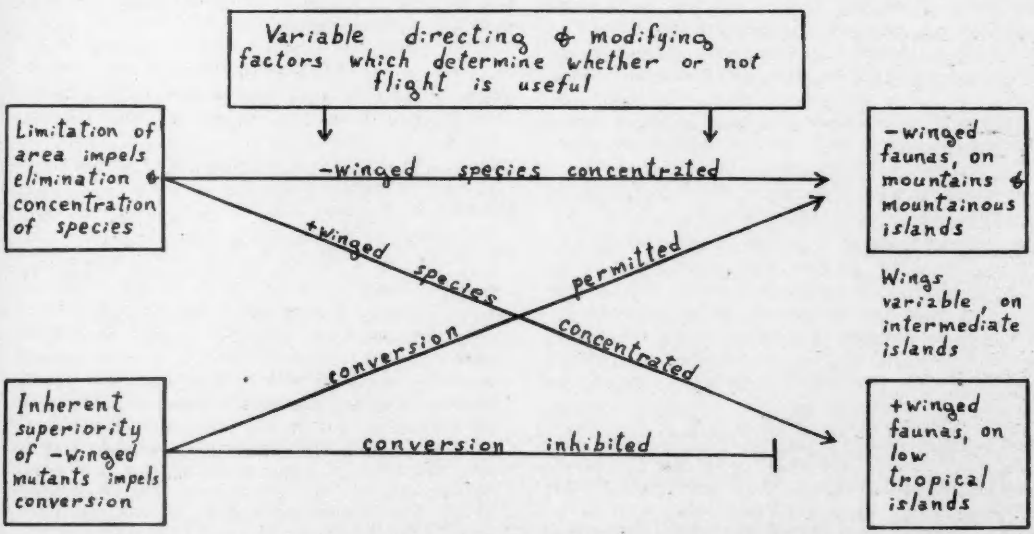

FIG. 8. Diagram to show how identical impelling forces, differently directed and modified by factors affecting usefulness of flight, may produce —winged Carabid faunas on mountains and mountainous islands, but +winged faunas on low tropical islands.

Large areas appear to be inhabited by many species with sparse, unstable populations; small areas, by fewer species, which must maintain denser, stable populations.

IV. The principal function of flight among geophile Carabidae is found to be to maintain sparse, unstable populations in large, unstable areas. In small, stable areas, where populations are dense and stable, flight presumably loses this function, permitting existence of flightless, —winged Carabidae, especially geophiles.

V. Occurrence of —winged Carabidae in nature is correlated with factors which tend to reduce usefulness of flight but which do not necessarily make it harmful. Atrophy of wings presumably involves selection of —winged mutants, which are usually selected not for flightlessness but for inherent simplicity and viability. This process may be supplemented by selection against flight where flight is harmful, and by non-selective genetic processes—by recurrence of mutation and by secondary effects of evolution of organs other than wings.

VI. Data are given on Carabid faunas of diverse mountains.

VII. In mountain Carabid faunas: (1) Species are few. (2) Most are geophiles; a few, brook-side hydrophiles; sometimes a few, arboreal. (3) Most of the geophiles and sometimes other species are —winged, as a result either of concentration of preexisting —winged stocks or of conversion of +winged stocks. Incidence of —winged species is usually *not* correlated with exposure. Predominance of —winged species is found not to be due simply to altitude, nor to exposure, nor to cold, nor to any simple direct factor, although cold may be indirectly involved. All characteristics of mountain Carabid faunas are due rather to complex factors inherent in mountain environments, thus: (1) Species are few because of limitation of habitats and of area. (2) Most are geophiles because limitation of habitats, supplemented by other factors, excludes hydrophiles (except brook-side species) and most arboreal forms. (3) *Concentration* of —winged species on mountains involves (a) elimination of +winged hydrophiles and arboreal species and concentration of geophiles, which are often —winged, and (b) further concentration of —winged species among geophiles. The latter process is impelled by limitation of area, which limits number of species even of geophiles on mountains and forces elimination and selection, and is directed by a combination of factors favoring —winged species. *Conversion* of +winged into —winged Carabidae is impelled mainly by selection of inherently superior —winged mutants, and is permitted to occur on mountains by factors which greatly reduce usefulness of flight.

VIII. Data are given on Carabid faunas of diverse islands.

IX. Island Carabid faunas share some characteristics of mountain faunas but are more variable. In island faunas: (1) Number of species is limited and varies with size of islands. This seems an effect primarily of limitation of area. (2) Geophiles are relatively numerous; hydrophiles and arboreal species, few, especially on small islands. This seems an effect of limitation not only of habitats but of area—geophiles probably more often than other Carabidae maintain dense, stable populations fit to exist in small areas. (3) Wings vary with nature of islands. On mountainous islands, most Carabidae are —winged, probably for the same reasons as on continental mountains. On intermediate islands, wings are variable. On low tropical islands, most Carabidae are +winged, probably because flight is useful on such islands, so that +winged species are concentrated and conversion inhibited.

In conclusion: facts here given contradict the old Darwinian idea that insects on mountains and islands are flightless, with atrophied wings, because flying forms are blown or straggle away from the exposed environments. On continents, —winged Carabidae occur where flight tends to lose its usefulness but not necessarily to be harmful (Sections IV, V). On mountains, they occur in sheltered as much as in exposed places (VI, VII). And on islands, their occurrence is correlated with mountainousness and coolness, not with exposure (VIII, IX). Everywhere, —winged Carabidae occur according to factors other than exposure, and wings appear to atrophy not by selection against flight but mainly by selection for —wingedness in places where flight is not useful. Whether or not flight is useful, and whether or not wings atrophy, depends on a balance of factors very much more complex than Darwin guessed. One factor especially stressed here is limitation of area, which exerts an indirect but profound effect on populations and on whole faunas, and ultimately on individual Carabidae. But the effect even of limitation of area is modified by other factors, probably especially by temperature.

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APPENDIX: LIST OF CARABIDAE RECORDED FROM THE PRESIDENTIAL RANGE ABOVE 3,000 FT.†

(—winged species)

Nomaretus bilobus: geophile; forest, rarely exposed
Sphaeroderus canadensis: geophile; forest
Sphaeroderus l. diffractus: geophile; forest
Sphaeroderus n. brevoorti: geophile; forest
Carabus c. groenlandicus: geophile; exposed (relict)
Notiophilus borealis: geophile; exposed (relict)
Notiophilus nemoralis: geophile; forest
Amerizus oblongulus: geophile; forest, rarely exposed
Patrobus f. tenuis: geophile; forest and exposed (relict)
*Trechus a. micans:** geophile; forest and exposed
Pterostichus adoxus: geophile; forest
Gastrellarius honestus: geophile; forest
Euferonia washingtonensis: geophile; forest, rarely exposed
Lyperopherus punctatissimus: geophile; forest, rarely exposed
Cryobius montanellus: geophile; exposed (relict)
Cryobius arcticola: geophile; exposed, rarely forest (relict)
Cryobius mandibularis: geophile; forest, rarely exposed
Calathus g. ingratus: geophile; forest, rarely exposed
Cymindis unicolor: geophile; exposed (relict)

(±winged species)

Carabus serratus: dimorphic lowland geophile: enters Presidential fauna (once) only as +winged straggler (Darlington 1936, pp. 142-143, 165).

Notiophilus aquaticus: dimorphic lowland geophile (name *aquaticus* is misnomer); enters Presidential fauna (erratically) only as +winged straggler (see Fig. 3).

Bembidion grapei: geophile; on Presidentials, exposed, rarely forest (relict). A northern, circumpolar species, known to be dimorphic in northern Europe and Siberia (Lindroth 1939a, pp. 77, 82) and in the Hudson Bay region and on islands in the Gulf of St. Lawrence (material in Museum of Comparative Zoölogy) as well as on the White Mts. On the latter: of 39 specimens from the Presidential Range, 35 are —winged, 4 +winged; of 4 from the smaller and lower exposed summit of Mt. Lafayette, 3 are —winged, 1 +winged; of 3 from the still lower exposed summit of Mt. Moosilauke, 1 is —winged, 2 +winged. This species is unknown in the lowlands of New Hampshire.

Tachyura granaria: dimorphic lowland geophile. Of 30 specimens examined from low altitudes in Massachusetts, New Hampshire, and Maine, 20 are —winged, 10 +winged. But 4 from the Presidential Range, above timber line, are all +winged; the species is apparently only a +winged, erratic straggler in the mountain fauna.

† See pp. 46 ff. for explanation and discussion.
* See also in list of dimorphic species, below.

Trechus apicalis micans: geophile; on Presidentials, both in forest and exposed. Range: eastern North America from Labrador to New Jersey, and farther south on the Appalachians; common in the White Mts., and fairly common also in lowlands. Until recently considered to be strictly —winged, but actually dimorphic: of 160 specimens examined, 159 are —winged, only 1 +winged (from Framingham, eastern Massachusetts, collected by C. A. Frost, in Fall Collection)! But since some 50 specimens examined from the Presidential Range are all —winged, I have allowed the species to stand as —winged on the Presidential list.

Micromaseus patruelis: dimorphic lowland geophile; enters Presidential fauna (once) only as +winged straggler (Darlington 1936, pp. 144, 165).

Platynus retractus: on Presidentials, a geophile, in forest (in lowlands, a facultative hydrophile). Dimorphic; most specimens even from low altitudes are —winged: *e.g.* of 35 examined from NE. Massachusetts, 29 are —winged, only 6 +winged. Of 28 from the Presidentials, 26 are —winged, 2 +winged.

Cymindis cribricollis: geophile; on Presidentials, in forest. Dimorphic; status of the species on the Presidential Range is not clear, but both —winged and +winged individuals are known from the White Mt. region (Darlington 1936, p. 147).

(+winged species)

Calosoma scrutator: once
Calosoma willcoxi: once
Calosoma frigidum: erratic
Calosoma calidum: once
*Carabus serratus:** once
Elaphrus clairvillei: hydrophile (swamps); forest and exposed
Elaphrus olivaceus: hydrophile (swamps); forest and exposed
Elaphrus cicatricosus: twice
Elaphrus fuliginosus: erratic
Elaphrus riparius: hydrophile (wet ground); forest and exposed
Blethisa julii: hydrophile (swamps); exposed, rarely forest (relict)
Blethisa quadricollis: erratic
Loricera pilicornis: hydrophile (swamps, etc.); forest and exposed
*Notiophilus aquaticus:** erratic
Nebria moesta: hydrophile (streams, etc.); exposed, rarely forest (relict)
Nebria suturalis: hydrophile (wet ground, etc.); exposed (relict)
Nebria lacustris: hydrophile (streams); forest, rarely exposed
Dyschirius globulosus: geophile; exposed (also open lowlands)
Bembidion edolatum: once
Bembidion simplex: hydrophile (streams); forest
Bembidion scopulinum: hydrophile (streams, etc.); forest and exposed (relict)
Bembidion posticum: hydrophile (wet ground); forest and exposed
Bembidion versutum: once
Bembidion arcuatum: hydrophile (wet ground); forest, rarely exposed
Bembidion versicolor: geophile; exposed (also open lowlands)
Bembidion sp.: geophile; exposed (also open lowlands)
Bembidion oberthuri: twice
Bembidion quadrimaculatum: geophile; exposed (also open lowlands)
Bembidion mutatum: geophile; exposed (also open lowlands)
Bembidion sulcatum: twice
Bembidion anguliferum: hydrophile (wet ground); forest and exposed
Tachyura incurva: twice
*Tachyura granaria:** erratic
Tachyta inornata: geophile; forest, rarely exposed
Platidius rugicollis: once
Poecilus lucublandus: geophile; exposed (also open lowlands)
Omaseus luctuosus: erratic
Dysidius mutus: erratic
Pseudargutor erythropus: geophile; exposed (also open lowlands)
*Micromaseus patruelis:** once
Bothriopterus luczoti: geophile; forest, rarely exposed
Cyrtonotus brunnipennis: geophile; exposed (relict)
Stereocerus haematopus: geophile; exposed (relict)
Leironotus arenarius: erratic
Leiocnemis avida: twice
Bradytus apricarius: twice
Bradytus latior: twice
Percosia obesa: erratic
Celia erratica: erratic
Celia chalcea: once
Celia brunnea: once
Amara impuncticollis: geophile; exposed (also open lowlands)
Amara cupreolata: geophile; exposed (also open lowlands)
Amara polita: twice
Triaena pallipes: geophile; exposed (also open lowlands)
Triaena angustata: geophile; exposed (also open lowlands)
Pristodactyla advena: geophile; forest, rarely exposed
Platynus stygicus: hydrophile (swamps, etc.); forest and exposed
Platynus sinuatus: geophile; forest
Platynus reflexus: once
Platynus piceolus: hydrophile (streams, etc.); forest, rarely exposed
Platynus tenuis: erratic
Platynus mutatus: erratic
Platynus molestus: twice
Platynus melanarius: twice
Platynus affinis: erratic
Platynus metallescens: hydrophile (swamps); forest and exposed
Platynus cupripennis: geophile; exposed (also open lowlands)
Platynus hardyi: erratic
Platynus excavatus: once
Platynus nutans: once
Platynus placidus: once
Platynus bogemanni: erratic
Platynus quadripunctatus: erratic
Platynus sordens: twice
Platynus lenis: twice
Platynus lutulentus: once
Casnonia pennsylvanica: once

* See list of dimorphic species above.

Lebia tricolor: twice
Lebia viridis: twice
Lebia moesta: once
Lebia pumila: erratic
Lebia ornata: once
Lebia fuscata: erratic
Lebia furcata: twice
Metabletus americanus: geophile; exposed (also open lowlands)
Miscodera arctica: once
Chlaenius purpuricollis: once
Chlaenius niger: twice
Chlaenius pennsylvanicus: erratic
Chlaenius tricolor: once
Brachylobus lithophilus: once
Harpalus viridiaeneus: erratic
Harpalus erythropus: once
Harpalus pennsylvanicus: erratic
Harpalus laticeps: erratic
Harpalus rufimanus: twice
Harpalus pleuriticus: geophile; exposed (also open lowlands)
Harpalus herbivagus: geophile; exposed (also open lowlands)
Harpalus proximus: twice
Selenophorus opalinus: twice
Triplectrus rusticus: twice
Anisodactylus harrisi: twice
Anisodactylus nigerrimus: once
Anadaptus baltimorensis: erratic
Anisotarsus terminatus: once
Spongopus verticalis: once
Trichocellus cognatus: geophile; exposed (relict)
Episcopellus autumnalis: twice
Tachycellus nigrinus: hydrophile (wet ground); forest and exposed
Tachycellus badiipennis: once
Tachycellus frosti: once
Catharellus cordicollis: once
Stenocellus rupestris: once
Stenocellus neglectus: geophile; exposed (also open lowlands)
Acupalpus carus: erratic
Stenolophus fuliginosus: hydrophile (wet ground); forest and exposed
Stenolophus plebejus: once
Stenolophus conjunctus: geophile; exposed (also open lowlands)
Tachystodes pauperculus: once
Agonoderus pallipes: once
Agonoderus comma: geophile; exposed (also open lowlands)

RESURVEY OF GRASSES, FORBS, AND UNDERGROUND PLANT PARTS AT THE END OF THE GREAT DROUGHT

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RESURVEY OF GRASSES, FORBS, AND UNDERGROUND PLANT PARTS AT THE END OF THE GREAT DROUGHT[1]

INTRODUCTION

Eight years have now passed since the fateful spring of 1934. The almost rainless March and April, the unusually high winds, and the great clouds of dust following two summers of decreasing precipitation, portended disaster. The intensity and duration of the drought and its appalling destruction have been studied from the beginning (Weaver, Stoddart, and Noll 1935) and several reports have recorded changes wrought in the native grass cover (Savage 1937; Weaver and Albertson 1936, 1939, 1940, 1940a). Drought began in great intensity a year earlier in the mixed prairie westward and southwestward. But previous to 1933, intensive studies had been pursued which gave a clear picture of the composition and structure of the several grassland types (Albertson 1937). Uninterrupted quantitative field studies year after year have traced the further deterioration or improvement of the meager vegetation until the wet year of 1941 finally concluded the dry cycle (Albertson and Weaver 1942).

The higher rainfall, sometimes monthly periods with three times the normal amount, has again moistened the dry soil to depths of normal, predrought root penetration. This, with a return to more normal atmospheric moisture, temperature, and wind movement, has already initiated marked changes in the vegetation. Hence, a resurvey of the condition of the vegetation of true prairie and mixed prairie, including its short-grass disclimax, both above and below ground at the end of the drought seemed advisable. It will conclude the phase of deterioration due to desiccation and at the same time provide a clear and definite background from which the processes involved in the return of vegetation to a new dynamic stabilization may be traced.

Detailed studies in true prairie have been made on 3 large grassland tracts in western Iowa and 12, each of 20 to 180 acres in extent, in eastern Nebraska and north-central Kansas. Nearly all of these have been examined regularly during each of the summer months of each year of the drought. Another group of 12 stations in the western half of Kansas has been similarly studied, although changes in some of them have been recorded for only 4 years. The writers have collaborated closely in all field work and especially on field trips sufficiently extensive to show clearly that the results here recorded apply in general to western Iowa, to much of Nebraska and Kansas (aside from sandy lands), and to the non-sandy soil of the eastern half of Colorado as well (Weaver and Albertson 1940a; Weaver and Mueller 1942) (Fig. 1).

Methods of study consisted of list, chart, clip, and permanent quadrats. Permanent transects and mapping, exclosures, and extensive trenching for root excavations have been employed. Much attention has been given to the reproduction, migration, and establishment of individual species of grasses and forbs, and considerable experimental work has been done on habits of growth, water relations, and relative drought resistance. Extensive histories of each prairie have been built up year by year and much work in other grassland areas over a wide range of territory has been done. This report will not include the very extensive measurements made on soil moisture and other habitat factors, since most of them have already been published. A comprehensive report on the conditions of growth and yield during the last dry year (1940) and the following wet one (1941) is included. For convenience of presentation and because the dominant grasses of true and mixed prairie are often different, their present condition in true prairie will be described first.

CONDITION OF GRASSES IN TRUE PRAIRIE

In true prairie, vegetation is so greatly disturbed that the general situation will be briefly outlined before the status of individual species is discussed. East of the Missouri River there has been little change and any damage to the vegetation has been almost completely repaired. West of this river the cover varies from small to large patches of almost predrought composition through all stages of deterioration to a condition where large areas of soil are only scantily clothed with vegetation. The undisturbed prairie remnants are often found on north-facing slopes or on low ground but also quite as often on level hilltops, on east or west slopes, or even on those facing southward. Why one portion of an apparently uniform area lost its vegetation by death, why the cover remained intact on the remaining part, and why half of the denuded area was again reclaimed and the other portion left nearly bare are unknown. Much thought and study have failed to reveal the answer in terms of habitat factors either above or below ground. The general course of destruction from upland down the sides of hills and then into ravines has been repeatedly observed, but why patches equally exposed were left intact remains unexplained (cf. Robertson 1939).

It has been repeatedly observed, however, that death of plants was directly correlated with depth of the root system, more shallowly rooted species almost invariably being the first to succumb. Vegetation in burned prairies was harmed most. But wherever the stand was more open or the soil poorly protected by

[1] Contribution No. 135 from the Department of Botany, University of Nebraska. This investigation was aided by a grant to the senior author from the Penrose fund of the American Philosophical Society.

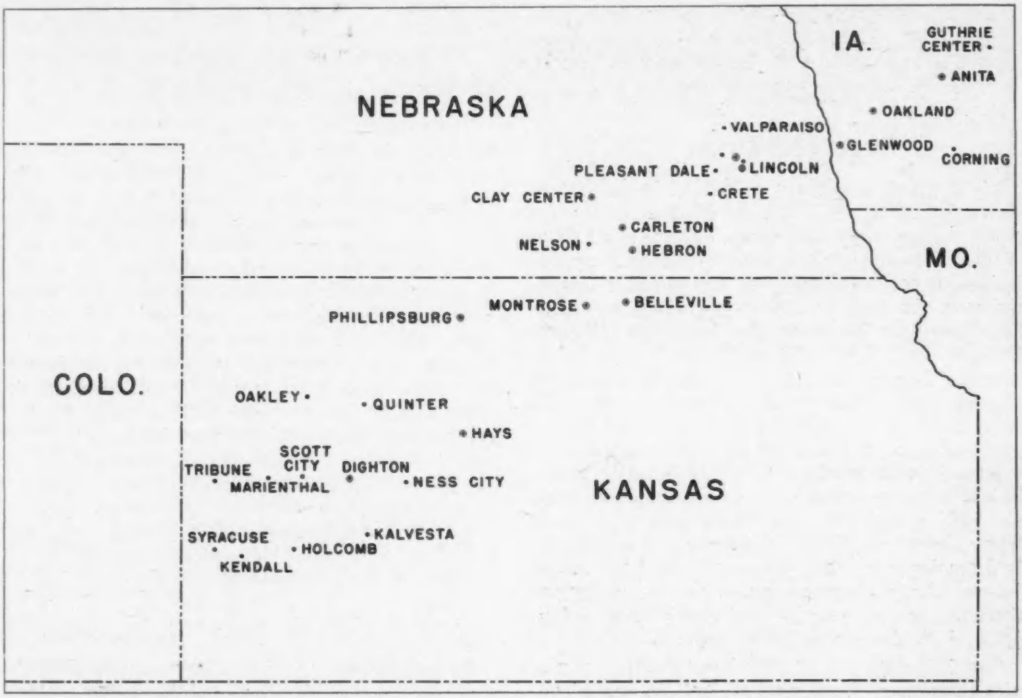

FIG. 1. Map showing location of stations where quantitative studies were made. Stations where water content of soil and plant yields were measured are indicated by a circle and dot, the locations of other stations are shown by dots only.

debris, small centers of bared soil appeared. Thus, the early losses were of the nature of openings in the prairie cover. Where drought was more intense, these open spaces were more abundant and formed a very irregular network of unoccupied soil surface. This openness of cover was greatly accentuated by great destruction to species of the understory. With succeeding years of drought the openings of moderate size often expanded into larger ones. Finally the cover was so decimated that the terrain appeared almost bare, with only the remnants of a former population (Weaver and Albertson 1936).

The spread of certain of the more xeric dominants and the great increase of species previously almost rare have been equally puzzling. Thus, certain bluestem prairies dominated by *Andropogon scoparius* and *A. furcatus* are now almost entirely covered with western wheat grass *(Agropyron smithii)*. Others are a mosaic of a complete cover of mixed relic bluestems, pure big bluestem *(Andropogon furcatus)*, blue grama *(Bouteloua gracilis)*, western wheat grass, and buffalo grass *(Buchloe dactyloides)*, each type occupying its portion or portions in almost pure stands. Ecotones are so sharply defined that the boundary lines of vegetation have been mapped with plane table and alidade to within a distance of three feet (Fig. 2). The open areas in other prairies with widely spaced plants and nearly bare soil are very irregular in shape and distribution (Figs. 3, 4, and 5). The total bare soil in some prairies would exceed by several times the part covered with vegetation. These are being repopulated by diverse species. Mixed communities which will include many dominants will develop for a time at least. Such mixtures constitute the present cover of numerous prairies or

FIG. 2. Three communities of native vegetation with sharply defined boundaries. In the foreground is buffalo grass and beyond is big bluestem. The background is a nearly pure stand of western wheat grass. Carleton, Neb., May 10, 1940.

FIG. 3. Bared area caused by drought in early stages of repopulation by blue grama. Valparaiso, Neb., July 8, 1938.

FIG. 4. Bared area in native grassland near Lincoln, Neb., in spring of 1941. Many of the smaller dead crowns of plants have been thrown out of the soil by frost heaving. This condition prevailed widely throughout the midwest after the winter of 1940-1941.

FIG. 5. Soil entirely bared by drought but partially repopulated by 2- and 3-year-old bunches of needle grass. Such conditions were common during the drought. Photo after mowing, Sept. 29, 1940, near Pleasant Dale, Neb.

the major portions of them. The transect and quadrats in Figure 6 are representative of this condition.

ANDROPOGON SCOPARIUS

Little bluestem, which was formerly the most abundant of all the prairie grasses, suffered the greatest loss. It is now of only intermediate importance and is outranked by six other species. Scarcely a trace remains in half of the 12 prairies, in others it is rare, and in only portions of two is it abundant. Conversely, in prairies of western Iowa it has maintained its former abundance and in some actually increased at the expense of big bluestem (Fig. 7). Most of the loss occurred the first year of the drought (1934) when great areas with 60 to 90 percent little bluestem alone were laid almost bare. Minor losses of weakened plants continued throughout subsequent years, especially in 1936. There was little or no noticeable recovery. Where the original stands were thinned, they were usually invaded by needle grass *(Stipa spartea)*, prairie dropseed *(Sporobolus heterolepis)*, blue grama, or western wheat grass, or partially repopulated by a spreading of big bluestem and side-oats grama *(Bouteloua curtipendula)* which formerly accompanied little bluestem.

ANDROPOGON FURCATUS

Although suffering great losses, big bluestem withstood the ravages of drought in a most remarkable manner. Even over the uplands, where it normally formed one fourth or less of the predrought cover, it frequently persisted even if in small amounts where all the little bluestem died. This is believed to be due to its deeper root system which absorbed enough moisture from 2 or 3 feet of moist earth below the level to which the soil was dried (about 4 feet) in 1934. The removal of its competitor (with roots averaging about 4 feet in depth) permitted full use of subsequent rainfall and the actual increase of this rhizomatous grass. At 7 of the 12 stations it is a chief dominant, although confined to certain areas; in the other prairies it remains only in a few very small patches, entirely surrounded by more drought-resisting and aggressive xeric grasses (Fig. 8).

Big bluestem formerly grew in nearly pure stands in well-aerated soil of moist ravines and at bases of slopes everywhere in true prairie. It formed a clearly demarked post-climax vegetation. In the drought region, these tall-grass areas have shrunk greatly in width and at their upper ends, often remaining as narrow belts. Big bluestem has frequently been replaced by western wheat grass, not only on higher land but also on lowlands moistened in part by run-in water. In some places whole hillsides of little bluestem and big bluestem prairie have first suffered the loss of the mid-grass, then undergone a thickening of the tall grass into a pure dense stand and finally the complete replacement of big bluestem by blue grama (Fig. 9).

As a final result of the 7 years of drought, big bluestem has lost greatly in the amount of soil it covered, other grasses entirely replacing it over great areas. It occurs irregularly on uplands in nearly pure stands to widely spaced bunches, and has its former percentage mixture with little bluestem in only a few relic patches. Its percentage relation to

STIPA SPARTEA

Distribution of needle grass before the drought was far less uniform than that of bluestems and many other grasses. It did not occur at any of the 6 most southwesterly stations, which is typical of its general absence in that area. But at the 6 eastern Nebraska stations the needle grass type of consociation was prominent and distinctly localized to hillcrests and dry slopes. Elsewhere it was represented, if at all, only as isolated bunches or patches in the other (usually little bluestem) types.

Needle grass, especially the oldest plants and the younger and hence more poorly rooted bunches, at first suffered greatly from the drought. Perhaps half the plants were killed. But once the survivors extended their roots into the new territory made available to water absorption by the thinning of the stand, their resistance to drought was greatly increased.

FIG. 10. Tufts of Kentucky bluegrass surviving as a result of shade produced by a small clump of ironweed *(Vernonia baldwini)* in a native pasture degenerated to bluegrass. April 20, 1935.

Needle grass renews growth early in spring, attains full development and ripens seed late in May in dry years. Then, by semidormancy, it evades the drought of summer but develops vigorously, if water is available, even late in fall. Almost every year some seed ripened, and during years of least drought it was produced in abundance.

A continuous spreading of this species has taken place into bared or semibared areas regardless of slope and even onto low ground. Seedlings from the deeply planted seeds have developed in abundance and many have survived. The single or few culms of first-year seedlings developed into a small bunch the second year and into a still larger one the third (Fig. 11). These clearly indicated the forward movement into territory formerly unoccupied by this species, the degree of aggregation, and the time relations as well. Today the new stands of needle grass occupy 5 to 10 times the area of the old ones, which are still extant. The vigorous early absorption of the meager available water supply by this species during drought has distinctly handicapped most other plants in these areas (Fig. 12).

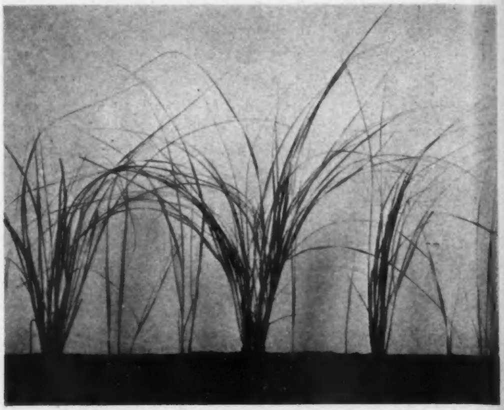

FIG. 11. Young plants of needle grass 1, 2, and 3 years old, transplanted from prairie into soft soil for photographing in August, 1939. The largest bunches are about 1.5 inches in diameter at the base and 14 inches tall.

SPOROBOLUS HETEROLEPIS

Prairie dropseed, like needle grass, did not occur at the most southwesterly group of true prairie stations. At the remaining stations, as over the true prairie generally, this type was more limited in dis-

FIG. 12. Little bluestem prairie greatly injured by drought and naturally reseeded to needle grass. June 16, 1941.

tribution than needle grass. But both large and small areas dominated by this dropseed in remarkably pure stands were available for study.

Early losses from drought were even higher than those of *Stipa spartea,* sometimes exceeding 85 percent. It seems probable that this late-blooming bunch grass had been greatly handicapped throughout the years by mowing during September before the seeds had ripened. During several of the years of drought, yield of grasses was so light that the prairies were unmowed or they were sometimes mowed in midsummer when the foliage began to wither. Under either treatment and in protected experimental areas the large seeds of this xerophyte were frequently produced in great quantity. Much soil, bare or only scantily covered with short-lived annual grasses and forbs, was available for occupation. Here prairie dropseed spread rapidly and has now become fully established in nearly pure stands. Increase has amounted in some prairies to 10 or more times the original area occupied, but elsewhere a heterogeneous mixture of widely spaced bunches of this species with those of needle grass, big bluestem, or mats of blue grama, and clumps of tall dropseed *(Sporobolus asper)* occur (Fig. 13).

FIG. 13. Bunches of prairie dropseed in early fruiting stage on September 5. Flower stalks are about 30 inches tall. Bunches are of only moderate size.

SPOROBOLUS ASPER

Tall dropseed was frequently a constituent of prairie vegetation, the plants or small bunches, if present, usually occurring as scattered individuals. It is a xeric grass which readily increases in abundance even in dry soil. Hence, its great increase in wide areas open to invasion as a result of drought was expected. It is now present at least sparingly in all of the prairies and abundantly in some. The bunch habit, mid-grass stature, erect, persistent flower stalks, and long-enduring, bleached, fibrous leaves, make it a conspicuous feature of the landscape (Fig. 14). Although it has increased greatly, especially in the most disturbed prairies, it is still among the least important of the 10 grasses of highest rank.

AGROPYRON SMITHII

Western wheat grass has made a phenomenal increase from a species of very minor importance to one of first rank. It alone has almost complete control of 3 of the 12 prairies, occupies about half of 5 others, and covers a third to a fifth of the remainder. The areas can be stated definitely since this sod-forming species is usually found in practically pure stands. Immediately after 1934, this wheat grass became increasingly abundant in prairies and native pastures. It has continued its spread over all types of terrain wherever bared places or open stands of other grasses had resulted from the terrible drought. Long, narrow belts of western wheat grass around the brows of hills indicated where early drought was most severe. Often the whole hillside was rapidly covered with a pure stand of this grass. Many lowlands, once occupied by big bluestem, are a continuous sea of undulating wheat grass. Seed was spread widely by wind and rodents. From newly established centers or along the edges of areas already invaded, slender, much-branched rhizomes 2 to 4 feet long grew rapidly during favorable times through the bared, mellow soil. During years with good spring and early summer rainfall great gains were made. A dry spring resulted in smaller advances of the invader. It is now found almost everywhere, regardless of soil, slope, or exposure. The only necessary conditions, aside from the presence of seed, seem to be those of weakened vegetation and unoccupied soil (Fig. 15). Only once has wheat grass been observed invading stabilized bluestem prairie.

FIG. 14. Bunches of tall dropseed in drought-damaged prairie on May 25, 1939. These grew the previous year but have maintained their erect form and bleached leaves over winter.

At first the new stands are thin but the stems are tall and heading is profuse. In a year or two the culms thicken to dense stands of 1,000 to 1,300 per square meter, each unit area being occupied by many

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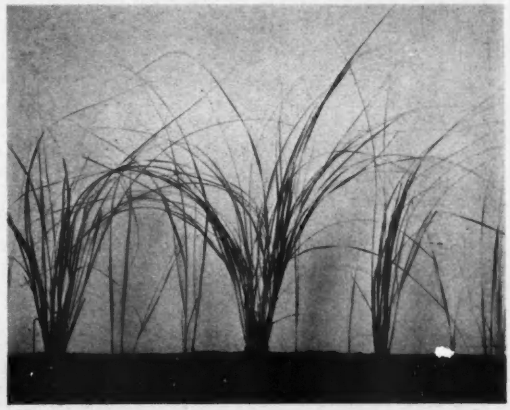

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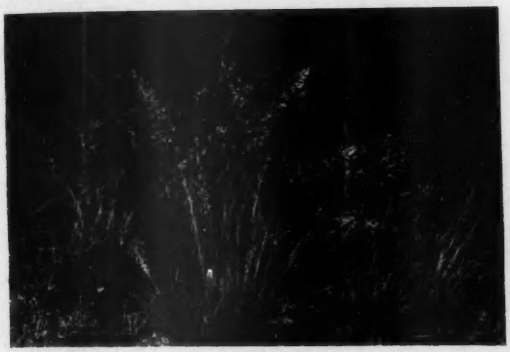

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SPOROBOLUS ASPER

Tall dropseed was frequently a constituent of prairie vegetation, the plants or small bunches, if present, usually occurring as scattered individuals. It is a xeric grass which readily increases in abundance even in dry soil. Hence, its great increase in wide areas open to invasion as a result of drought was expected. It is now present at least sparingly in all of the prairies and abundantly in some. The bunch habit, mid-grass stature, erect, persistent flower stalks, and long-enduring, bleached, fibrous leaves, make it a conspicuous feature of the landscape (Fig. 14). Although it has increased greatly, especially in the most disturbed prairies, it is still among the least important of the 10 grasses of highest rank.

AGROPYRON SMITHII

Western wheat grass has made a phenomenal increase from a species of very minor importance to one of first rank. It alone has almost complete control of 3 of the 12 prairies, occupies about half of 5 others, and covers a third to a fifth of the remainder. The areas can be stated definitely since this sod-forming species is usually found in practically pure stands. Immediately after 1934, this wheat grass became increasingly abundant in prairies and native pastures. It has continued its spread over all types of terrain wherever bared places or open stands of other grasses had resulted from the terrible drought. Long, narrow belts of western wheat grass around the brows of hills indicated where early drought was most severe. Often the whole hillside was rapidly

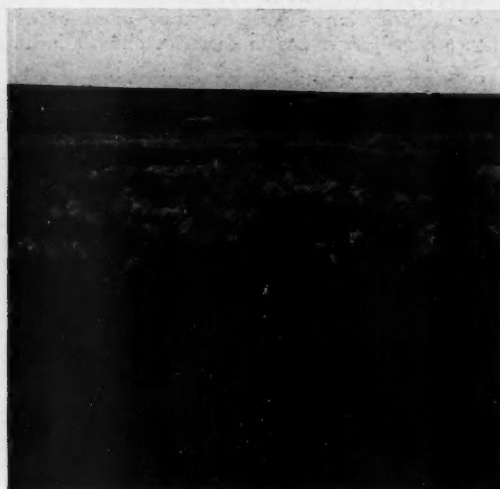

FIG. 14. Bunches of tall dropseed in drought-damaged prairie on May 25, 1939. These grew the previous year but have maintained their erect form and bleached leaves over winter.

covered with a pure stand of this grass. Many lowlands, once occupied by big bluestem, are a continuous sea of undulating wheat grass. Seed was spread widely by wind and rodents. From newly established centers or along the edges of areas already invaded, slender, much-branched rhizomes 2 to 4 feet long grew rapidly during favorable times through the bared, mellow soil. During years with good spring and early summer rainfall great gains were made. A dry spring resulted in smaller advances of the invader. It is now found almost everywhere, regardless of soil, slope, or exposure. The only necessary conditions, aside from the presence of seed, seem to be those of weakened vegetation and unoccupied soil (Fig. 15). Only once has wheat grass been observed invading stabilized bluestem prairie.

At first the new stands are thin but the stems are tall and heading is profuse. In a year or two the culms thicken to dense stands of 1,000 to 1,300 per square meter, each unit area being occupied by many

miles of roots and rhizomes. Dwarfing of the foliage and scarcity or absence of spikes indicate at once the low supply of soil moisture and the clue to the wilting, dwarfing, or death of relic bluestems and other less xeric grasses and forbs. Thus, the threading of the rhizomes between the bunches of relic vegetation, indicated by the widely spaced new stems of wheat grass, foreshadowed its final destruction where drought continued. Blue grama and, in a lesser degree, side-oats grama are not ousted by the invader. Neither is needle grass successfully invaded.

The early growth of both western wheat grass and needle grass and consequent depletion of soil moisture by transpiration are important factors in their spread during drought. An experiment to compare rate of water loss from small areas of little bluestem, wheat grass, and needle grass was performed early in the spring of 1941. Circular pieces of undisturbed sod 18 inches in diameter and 10 inches deep, with natural cover undisturbed, were transferred in pairs into 6 galvanized iron containers 2 feet deep. These had previously been partly filled with moist, compacted prairie soil, so that when the sods were firmly in place they entirely filled the containers to within 2 inches of the top. Containers were weighed March 25 and placed out-of-doors in a frame of 2-inch planks, with insulation between them and the frame. Rainfall was measured and enough extra water added at subsequent weighings as needed to maintain conditions favorable to growth (Fig. 16). The results are shown in Figure 17.

Fig. 15. Alternes of western wheat grass in unmown little bluestem prairie at Hebron, Neb., on May 10, 1940, before other vegetation had made much growth.

Loss of water by transpiration and evaporation from the soil surface was much less from the bluestem which began growth at its normal time, about April 15. The late spring delayed growth of western wheat grass and needle grass at least two weeks. But despite this, total loss from each of these grasses (86.65 and 90.15 pounds, respectively) was more than twice as great as the 41.55 pounds from little bluestem. Similar field experiments by R. J. Weaver (1941) the preceding spring gave similar results.

Fig. 16. (Lower) Development of grasses on April 25. New shoots of *Andropogon scoparius* (left) average an inch in height but only half of the sod is green. Western wheat grass (center) is 7 inches tall and in the fourth-leaf stage; needle grass (right) likewise is growing rapidly.

(Upper) Development on May 20. Little bluestem is only 6.5 inches tall; western wheat grass is 20 inches high and in the eighth-leaf stage; the spikes are just appearing. Needle grass has some flower stalks well developed and the awns of the fruits are emerging from the sheath.

Grasses with rapid development in early spring and with early maturity evade midsummer drought. These same grasses grow vigorously in autumn even after most others are mature and the foliage often no longer green. Clearly, late-appearing grasses are at a great disadvantage and may succumb, when

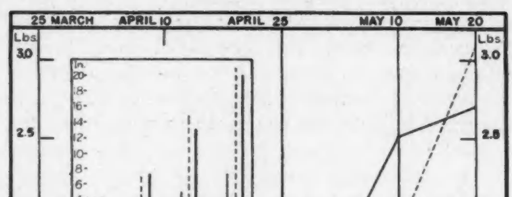

Fig. 17. Average daily loss in pounds per container of *Agropyron smithii* (heavy line), *Stipa spartea* (broken line), and *Andropogon scoparius* (light line), during the spring of 1941. Date of renewal of growth is indicated by X. The insert shows average height of grasses on the several dates indicated.

summer rainfall is very light, from lack of soil moisture used by competitors with different growth habits.

It has been shown elsewhere, as a result of many experiments, that under a cover of wheat grass the rate of infiltration of water into the soil is slow. It averaged 2.4 times as rapid in bluestem prairie as in western wheat grass a few feet distant (Weaver 1942).

BOUTELOUA CURTIPENDULA

Side-oats grama is a very drought-resistant grass. It often persisted where all other mid-grasses succumbed. It usually has the appearance of a bunch former, but its abundant rhizomes which are 2 to 4 inches long enable it to spread rapidly. Moreover, it is a prolific seeder, and its range of habitat from moist to dry sites is very wide. Only a grass with such characteristics could increase so rapidly, even if widely and uniformly distributed, from its pre-drought abundance of only about 0.5 percent of the basal cover to a species of the first rank (Fig. 18).

FIG. 18. Representative bunches of a stand of side-oats grama which covered much bared ground following the early years of the great drought. The plants are about 3 feet tall. Nelson, Neb., Aug. 12, 1937.

Approximately one fifth to one third of the vegetation at most of the 12 prairies consists of this species, except in the portions dominated by western wheat grass, and even in wheat grass prairies it is prominent during years with at least moderately good rainfall.

Side-oats grama is fully as important as needle grass, with which it is intermixed, but it rarely shows such a high degree of dominance as this species. It is far more widely distributed throughout the prairies than is needle grass and has replaced little bluestem to an even greater extent than has big bluestem. In certain prairies it has attained the rank of the leading dominant, and over considerable areas where bluestems were killed by burial under dust it grew during the most favorable drought years in pure dense stands. In fact, it seems to have overdrawn on the water supply and suffered from drought in consequence. In some places it was severely handicapped by disease (Fowler and Weaver 1940).

In many drought-swept prairies, increase of side-oats grama occurred synchronously with the spreading of western wheat grass into the bared areas or into stands of relic big bluestem. The following years witnessed the death of big bluestem but only the suppression of side-oats grama during dry summers. When rainfall in early spring was adequate for good growth but early summer was dry, wheat grass thrived. When early spring was dry and late spring and summer moist, side-oats grama flourished even in a thick stand of wheat grass. In many local areas it has almost replaced its competitor; in others, the reverse is true, while elsewhere almost equal mixtures of these two dominants prevail.

In native pastures, mixed pasture types in the Dakota-Nebraska-Kansas area have resulted from the great increase in side-oats grama and an eastward spreading of sand dropseed *(Sporobolus cryptandrus)* and western wheat grass. These grasses are often intermixed, especially side-oats grama with sand dropseed or western wheat grass, or each of the three species may dominate different portions of the same pasture.

BOUTELOUA GRACILIS

Blue grama is now so abundant and has spread so widely that its great gains can be appreciated only by comparison with its former limited occurrence. In 1934, Weaver and Fitzpatrick described it as "sometimes found on thin soils on brows of the steeper hills, especially the xeroclines, occasionally on much eroded, steep slopes bordering ravines, . . . in the drier parts of the [true-prairie] region. Here it may occur only as scattered tufts or it may dominate local areas. Its increasing abundance in the understory in undisturbed grassland is an indication of the proximity of the mixed prairie." Little wonder that with death or thinning of its mid-grass competitors and the impact of a Great Plains climate for a period of years over the western edge of true prairie, this dry-land species flourished (Fig. 19). Blue grama is the most drought-resistant of all the native grasses of the Nebraska-Kansas-Colorado region (Mueller and Weaver 1942). It has been more widely and more consistently represented by seedlings and especially seedlings that survived than any other species (Weaver and Mueller 1942). It has often survived where all other grasses have died and repopulated the adjacent bared areas with abundant seedlings (Figs. 3 and 20).

Blue grama spread promptly following the initial drought, since it was harmed the least of all species. Wind and surface water carried the seeds down the slopes and by intermixing them with soil aided in their planting. In this way new centers of distribution were started. By means of peripheral growth from old and new clumps, territory was gained even during years so dry that most grasses merely sur-

Fig. 19. Invasion of blue grama (light color) into territory occupied by drought-depleted little bluestem. Unmown prairie at Lincoln, Neb., April 29, 1939.

vived. Hence in the grasslands today, patches of blue grama both large and small are to be found anywhere except where the original cover of mid grasses prevailed. Small patches have often become very large and transitions from this short grass to mid grasses or even to the tall big bluestem are often sharp.

Conversely, pioneer tufts and isolated young sods may occur among widely spaced relic or young bunches of tall dropseed, needle grass, big bluestem, or side-oats grama—in fact among any species that remained or has become established in these broad areas ravaged by drought. Such a mixture would not have been understandable in the years before this catastrophe.

During a period of 5 years, flourishing stands of wheat grass have been gradually replaced where blue grama seedlings became well established (Fig. 21). This was a process of gradually thinning the stand as the many centers of blue grama slowly became larger and finally merged and formed an almost complete cover. The short grass has a much finer root system than that of western wheat grass and it more thoroughly occupies the soil, especially near the surface. This grass also has the great advantage of growing vigorously at any time during the warm season, regardless of previous seasonal activity. Its flower stalks can develop, blossoms appear, and seeds ripen in only a few weeks. Hence, it successfully invades pure stands of western wheat grass.

Fig. 20. Extension of blue grama from a few parent clumps to form a more or less continuous cover on hilltop and upper slopes at Valparaiso in eastern Nebraska. April 15, 1941.

Conversely, old stands of blue grama have been invaded in favorable years by western wheat grass. This produced a type of mixed prairie very common before the drought, especially northwestward. By this invasion a more or less stable community of mid- and short grass has now been formed, especially in native pastures. This type had no former place in true prairie and its spread, often in combination with buffalo grass, eastward to within 40 miles of the Missouri River is a direct result of the marked arid phase of the climatic cycle.

Fig. 21. This entire area at Hebron, Neb., was occupied by bluestem grasses in 1934. As a result of drought and drifting dust they were replaced by western wheat grass by 1936. Much of the wheat grass was, in turn, replaced by blue grama by 1940. May 10, 1940; dark areas are wheat grass and light-colored patches blue grama.

Buchloe Dactyloides

Buffalo grass was far less abundant than blue grama before the great drought. It occurred sparingly, sometimes in pure, dense mats of limited extent in ravines but was more usually associated with blue grama on the thinner upland soils. It survived the drought much more poorly than blue grama. It occurs in the 6 westerly prairies, but in 3 only sparingly. In the other 3 it has spread widely, sometimes in pure stands but more often intermixed with blue grama. Many of the more open stands have been invaded by western wheat grass and have become mixed prairie locally (Fig. 22). Perhaps the mellowing of the surface soil by freezing and thawing, following the opening of the plant cover by drought, has been unfavorable to its spread. In native pastures half bared by trampling, it has made great gains and now often clothes the soil with nearly pure stands, thus presenting vegetation of the Great

Plains disclimax far into true prairie. Of course, this occurred even before the drought, but short-grass pastures along the western margin of true prairie have greatly increased in numbers and in total area. They occur as far eastward as the Big Sioux River in South Dakota and are also found in extreme southwestern Minnesota. In southern Nebraska they are common to within 40 miles of the Missouri River.

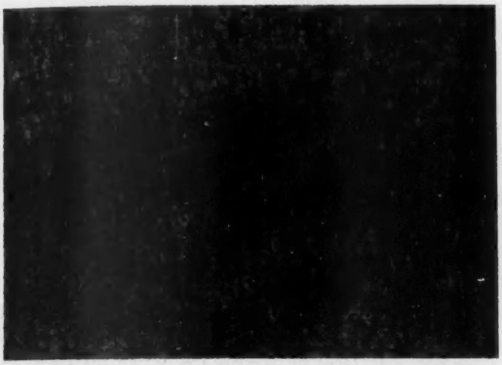

FIG. 22. Mixed prairie resulting from the mid-grass, *Agropyron smithii*, invading territory occupied by the short grass, *Buchloe dactyloides*. Carleton, Neb., May 10, 1940.

OTHER CLIMAX GRASSES

Abundance of June grass *(Koeleria cristata)* is more difficult to evaluate than that of most other species. This is because of its greater instability and shorter life span. It was greatly harmed by the drought. The root system is shallow (15 to 28 inches) and its decided predrought occurrence on dry uplands resulted in great losses. But quantities of seed on the soil aided in quick reestablishment of this species of boreal origin during the following spring and early summer. In fact, certain prairies which lost heavily were quickly repopulated by nearly pure stands of June grass only to be bared once more when extreme drought struck again. Thus, while June grass has increased generally at several periods, its gains seem temporary. Large, persistent bunches are rarely found. It is a drought evader profiting by early growth, summer dormancy, and autumnal development, as well as by decreased competition. It is found mostly where vegetation is very open, and little occurs in stands of western wheat grass or bluestem prairie. There was much less June grass at the end of the drought than at its outset.

Pennsylvania sedge *(Carex pennsylvanica)* has, of course, the grass life form and may be considered here. It was a minor component of the vegetation, but locally, as on dry ridges, it sometimes formed 5 to 10 percent of large areas and in very limited ones as much as one third or more of the plant cover. It is drought-resistant and has gradually increased. Sometimes it forms nearly pure stands in patches many square yards in extent, more often its increase has been general and it is now scattered as before throughout the prairie but in very much greater abundance.

Plains muhly *(Muhlenbergia cuspidata)* was formerly so rare that it was not mentioned in the monograph on prairie among the 50 minor grasses. This drought-resistant, western species has gradually migrated eastward and increased in prairie and pasture until it is no longer uncommon. In fact, it forms small pure stands on many dry hills and xeric slopes (Fig. 23).

Sand dropseed *(Sporobolus cryptandrus)*, following the early years of drought and consequent widespread losses of pasture grasses, has increased rapidly in pastures from the status of an occasional invader to a species of major importance. Over thousands of ranges it has spread so widely as to become a dominant or the dominant species. It has repopulated vast areas left nearly bare by the death of bluegrass, little bluestem, and other pasture plants. This western species has given stability and good productivity to pasture lands too dry for more mesic grasses. These facts are essential to an understanding of its invasion of the bared areas in prairie. This took place only slowly and only during the latter years of drought. In true prairie this bunch grass plays the part of a preclimax dominant. It has entered the prairie only in the bared places and only in relatively small amounts.

FIG. 23. Pure stand of *Muhlenbergia cuspidata* on the crest of a ridge at Nelson, Neb., June 16, 1939.

Tall panic grass *(Panicum virgatum)*, nodding wild rye *(Elymus canadensis)*, and slough grass *(Spartina pectinata)* have retained their former abundance on lowlands with a rather constant supply of ground water or water from runoff. Such places, however, are relatively few. In general, there has been a great shrinking of the territory in ravines and lowlands occupied by these species. Frequently they have been replaced by big bluestem, as soil aeration was improved, or by western wheat grass. Clearly, all three of these meso-hydrophytes have greatly decreased.

Annual Grasses

Immediately following the drought, the bared soil, exposed to erosion by wind and water, was populated thinly to thickly by annual grasses and other weedy species. Chief among the grasses were six-weeks fescue *(Festuca octoflora)*, chess *(Bromus secalinus* or closely related species), and little barley *(Hordeum pusillum)*. These sometimes covered whole hillsides in dense stands (Weaver and Albertson 1936). *Bromus tectorum* and *Panicum capillare* were other abundant ruderals of wide distribution. In general, the bared or semibared areas were largely reclaimed by long-lived grasses or by certain native forbs. Thus, later in the drought years these annual grasses, where present, chiefly occupied the smaller interspaces and, with rare exceptions, were not found in large belts or patches as formerly.

Studies on the Composition of Plant Cover

An extensive quantitative survey of the total basal cover in the little bluestem type of vegetation was made near the end of the drought. This consisted of a total of 100 quadrats rather uniformly distributed among 10 different prairie areas widely scattered in eastern Nebraska. The basal or ground cover is the actual area occupied by the stems, mats, or tufts of plants about an inch above the soil surface. It was determined by estimating the area occupied in each square decimeter of each quadrat separately. The average of the 100 estimates gave the percentage of basal cover of the entire square meter. The quadrats were taken at random in the same general locations where similar studies had been made in 1929-1931. They included level land, hillcrests, and all slopes which were earlier dominated by little bluestem.

The average basal area before the drought was 13.6 percent. The second survey, in 1938, showed that it was only 5.1 percent or about 38 percent of the former amount. There were, of course, considerable variations from the mean; in fact these variations were somewhat greater than those found in the predrought survey (Weaver and Fitzpatrick 1934).

This survey also included the percentage of basal cover composed by various grasses or by forbs in these same quadrats. Methods were the same as those employed before the drought, strips of 20 square decimeters being the unit portion of the quadrat used for each estimation, that is, 5 separate estimates were made in each square meter. This was invariably done by two investigators accustomed to the use of this method (Table 1).

Table 1. Percentage of basal cover in the *Andropogon scoparius* type composed of various grasses and forbs. Arrangement of species is in the order of their predrought importance. First column, 130 quadrats in the general area west of the isohyet of 32 inches, where data were obtained in 1929-1931, previous to the drought; third column, 100 quadrats in eastern Nebraska in 1938; second column, 50 quadrats from the same eastern Nebraska prairies as those sampled in column three but taken before the drought.

Species	*Percent Cover*	*Percent Cover*	*Percent Cover*
Andropogon scoparius	56.2	55.0	5.1
Andropogon furcatus	23.1	19.4	17.9
Poa pratensis	5.8	4.9	5.8
Stipa spartea	3.1	1.6	9.7
Sporobolus heterolepis	2.8	7.1	11.6
Sorghastrum nutans	1.4	1.8	1.7
Bouteloua curtipendula	.7	.6	14.3
Koeleria cristata	.6	1.3	4.7
Panicum scribnerianum and P. wilcoxianum	.3	.3	.3
Panicum virgatum	.1	.0	.8
Forbs	4.2	4.6	11.3
Sporobolus asper		1.0	2.6
Bouteloua gracilis		.5	3.1
Carex pennsylvanica		.4	4.9
Agropyron smithii			1.9
Total	98.3	98.5	95.7

Comparison of the results from the general true-prairie predrought area (column one) with those of the predrought eastern Nebraska prairies (column two) shows, with exceptions, remarkably small differences. But a similar comparison of the quadrats in eastern Nebraska before and after the drought (columns 2 and 3) reveals marked changes. Chief among these is the great decrease in *Andropogon scoparius* (91 percent),[2] and the great increases in *Stipa spartea* (506 percent), *Sporobolus heterolepis* (63 percent), and *Bouteloua curtipendula* (2,283 percent). Increases of *Bouteloua gracilis, Carex pennsylvanica, Sporobolus asper,* and forbs were 520, 1,125, 160, and 146 percent, respectively. *Andropogon furcatus* decreased slightly but *Poa pratensis* increased somewhat. No quadrats were located where the invasion of *Agropyron smithii* was much in evidence. The remaining portion of the total cover (4.3 percent) consisted of weedy annual grasses.

Seedling grasses and forbs were recorded as observed in June and July, 1938, in the 100 meter quadrats. A total of 1,008 seedling grasses was found. Among these the four species with the most seedlings were *Panicum wilcoxianum* (316), *Bouteloua curtipendula* (191), *Panicum scribnerianum* (169), and *Sporobolus heterolepis* (92). Twenty-three species of native forbs and 9 of weeds were represented by a total of 2,930 and 48 seedlings, respectively. Forbs with the most seedlings were *Erigeron ramosus* (2,098), *Senecio plattensis* (313), and *Aster multiflorus* (231). The very low rate of 1 grass seedling per 10 square decimeters was quite usual during the period of drought; frequently there was none (Weaver and Mueller 1942).

The quadrats in Table 1 do not represent the whole range of prairie stations, and are indicative of conditions in eastern Nebraska only. Repeated examination of the relative abundance of the various components of the prairie from the eastern border of drought-damaged true prairie to its replacement westward by mixed prairie gave a broader and dif-

[2] It should be made clear that this percentage is not the actual reduction in the amount of grass, which was much greater, but that little bluestem constituted 91 percent less of the total post-drought vegetation than it did of the total predrought cover.

ferent picture. This survey was made in 1940, at the close of the drought. According to their abundance and control over the habitat the grasses may be readily divided into four groups. Species in each group are arranged so far as possible in sequence of decreasing abundance.

1. Species of Major Abundance
   Agropyron smithii
   Bouteloua curtipendula
   Andropogon furcatus
   Stipa spartea
2. Species of Considerable Abundance
   Bouteloua gracilis
   Sporobolus heterolepis
3. Species of Intermediate Abundance
   Andropogon scoparius
   Koeleria cristata
   Sporobolus asper
   Buchloe dactyloides
   Poa pratensis
4. Species of Minor Abundance
   Muhlenbergia cuspidata
   Panicum scribnerianum
   Sorghastrum nutans

CONDITION OF GRASSES IN MIXED PRAIRIE

Three general types of vegetation, with varying degrees of intermixtures, have been described for western Kansas as they appeared before the drought (Albertson 1937). The little bluestem consociation occupied hillsides, where rock outcrops were common, as well as shallow ravines. It also extended over the brows of the hills and far beyond where the slopes continued, but gave way more or less abruptly to short grasses on level uplands.

Little bluestem alone constituted nearly half of the vegetation. In drier places it formed distinct bunches, but a nearly continuous sod-mat in wetter ones. Numerous tall grasses, as *Panicum virgatum* and *Sorghastrum nutans* and the mid-grass, *Bouteloua curtipendula,* were common, the roots usually penetrating deeply into the rock crevices.

The postclimax big bluestem consocies covered lower slopes, the lowland, and deep ravines where water from rainfall was supplemented by the melting of wind-drifted snow and especially by runoff water from the higher land. Big bluestem alone usually composed 75 percent of the vegetation. Its chief associates were *Bouteloua curtipendula, Agropyron smithii,* and *Sporobolus asper* var. *hookeri,* but tall grasses also were common, especially in wetter sites. All were rooted 5 to 7 feet deep in the rich alluvial soil.

The short-grass faciation was found widely distributed over the nearly level uplands where the soil, watered by precipitation only, had developed a mature profile. Westward from Phillipsburg and Hays vast areas of range lands were characterized by the dominance of *Bouteloua gracilis* and *Buchloe dactyloides.* These grasses usually composed 80 to 90 percent of the vegetation. They occurred in almost equal amounts in the closed-mat type near Hays where the basal cover varied from 70 to 90 percent, a condition not uncommon over hundreds of square miles of the Great Plains disclimax. In the open-mat type

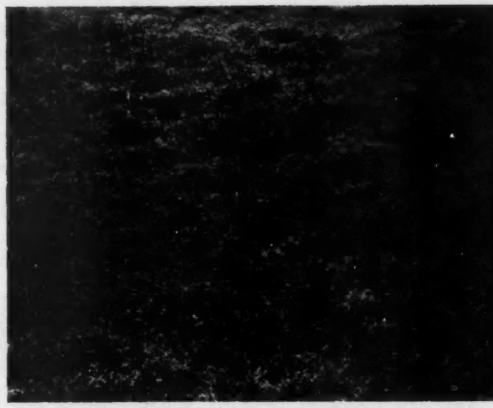

FIG. 24. A typical stand of mixed short grasses of the closed-mat type, which formed excellent cover previous to the dry years.

of depressions with decreased water infiltration and of thin soil, the basal cover was more commonly only 10 to 33 percent. Under such conditions blue grama frequently predominated (cf. Shantz 1911). Where the short-grass sod was best developed there were practically no plants which rose above the 3- to 5-inch level of the foliage. But certain low-growing annuals were normal components of the vegetation, as *Hordeum pusillum, Festuca octoflora, Plantago purshii,* and *P. spinulosa.*

Although all three types of vegetation recur repeatedly where topography is sufficiently rolling to present the proper conditions of habitat, the short-grass type is by far the greatest in extent.

Drought and dust have wrought great changes not only in the composition but also in the amount of vegetation (Figs. 24 and 25). They have also caused

FIG. 25. Vegetation, previously similar to that shown in Figure 24, near the end of the great drought. Note wide spacing of relic tufts, bared soil without mulch, and elevation of the plants somewhat above the general surface, the top inch of soil having been blown or washed away.

great changes of vegetational boundaries between grassland types. Movements of grass populations have been from the more xeric toward the less xeric habitats. In many places the only plants that survived were those in moister places such as buffalo wallows, ditches, and ravines. Reduction of cover to 2 to 10 percent was not uncommon. Frequently large areas of nearly level grassland were covered with several inches of dust, brought by the wind from adjacent cultivated fields. Under extreme conditions the wind-blown soil formed long, tortuous drifts under which the native vegetation was buried and completely destroyed.

Andropogon Scoparius

Before the drought, little bluestem ranged far out from its hillside habitat into the short grasses on the tablelands. Here it occurred widely scattered as isolated bunches or in small patches. It was here that the first effects of the drought became apparent and only dead crowns of this species remained after 1934. Even in its own type, this species was materially reduced, being replaced chiefly by side-oats grama and blue grama. At the end of the drought period only occasional bunches of little bluestem could be found even on north-facing slopes or in depressions on the hillsides where runoff water accumulated. Thus, this dominant was reduced from about 45 percent of the total vegetation to only 1 percent. It also practically disappeared from the "hard lands" westward and was found only rarely.

Andropogon Furcatus

Big bluestem not only dominated the bottoms of ravines and lowlands but was also scattered throughout the little bluestem type on the hillsides. The effect of the drought upon this species became evident somewhat later than upon most other grasses associated with it. On the hillsides where little bluestem was dominant, big bluestem, due to a somewhat deeper root system, was able to survive with little loss several years after little bluestem died. But during the later years of drought it was reduced in area occupied to only one fourth of its predrought abundance. On the lower slopes and in ravines where big bluestem was dominant, the total cover of grass was not significantly decreased but merely changed in composition. It was here that large areas of nearly pure big bluestem, so common before the drought, were almost entirely replaced by other species such as western wheat grass, dropseed *(Sporobolus asper* var. *hookeri)*, side-oats grama *(Bouteloua curtipendula)*, and even by buffalo grass and blue grama grass. Thus, at the end of the drought its abundance was often only about one fifth of the normal.

Bouteloua Curtipendula

Side-oats grama had a wide predrought distribution in the mixed prairie. It was a chief associate of big bluestem in the postclimax type of grassland where it was a dominant species. Its bunches were also scattered widely throughout the little bluestem type on the hillsides, and it was one of the four important mid-grasses that extended into the short-grass type more or less throughout western Kansas, eastern Colorado, and adjacent areas. But by the end of the drought even this xeric species was enormously reduced in numbers and over a wide territory it entirely disappeared from among the short grasses. Conversely, it made steady gains in the little bluestem type and was the chief invader of the soil left bare by the death of little bluestem (Fig. 26). An increase in amount of two- or threefold was usual. Likewise, in the ravines and on lower slopes it frequently replaced big bluestem.

Fig. 26. Dense stand of side-oats grama which has largely replaced little bluestem on the hillsides. Hays, Kan., Sept. 8, 1939.

Aristida Purpurea and A. Longiseta

The wire grasses were most abundant and most permanently entrenched along hillsides in the little bluestem type. They also extended widely and often abundantly over the short-grass disclimax. The pattern was variable according to type of soil and degree of disturbance. On the heavier silt-loams or very fine sandy loams these low bunch grasses were few, but they increased with coarser sand content of soil, and were often of great abundance in subseres (Fig. 27). Upon the advent of the drought, these shallowly

Fig. 27. Bunches of wire grass *(Aristida purpurea)* in short-grass sod near Colorado Springs, Colo., preceding the dry cycle of 1933-41.

rooted grasses were among the first to show the effects of decreased water content. By 1935 only their dead crowns could be found in the short-grass type. Even on the hillsides they suffered a high rate of mortality and persisted only in places that were protected by some form of vegetation or as a result of irregular topography.

BOUTELOUA GRACILIS

Blue grama with its codominant, buffalo grass, constituted fully four fifths of the entire vegetation in the short-grass type. This predrought turf, with small openings scattered throughout, has received so much abuse from edaphic and atmospheric drought, dust, overgrazing by domesticated animals, jack rabbits, and grasshoppers, that it is now composed of nearly isolated remnants of sod in a wilderness of bared soil. Yet the present vegetation, sorely depleted as it is, consists almost entirely of these same two short grasses. Thus, during the stress of drought most of the blue grama was killed, but that which remained grew in small tufts or bunches a few inches to many feet apart (Fig. 25). In places where run-off was great, large tracts of many square rods were completely denuded of this grass and all other vegetation. Other vast areas were bared or almost denuded by a covering of dust. In contrast to these losses which ranged from 50 to 100 percent, gains were made by blue grama spreading on hillsides and into upper ravines where certain mid-grasses had succumbed. In fact, most lowlands were also occupied by this grass.

BUCHLOE DACTYLOIDES

Buffalo grass often shared the soil more or less equally with blue grama before the great drought. In many places this stoloniferous grass entirely disappeared from the mixture during the early years of desiccation, and in practically no location was it damaged only lightly. During the short periods with moist soil, the stolons developed rapidly where this grass remained, often an inch per day, but usually the new growth was killed by succeeding dry periods. The gains and losses of buffalo grass during this period of adversity fluctuated to a much greater extent than did those of blue grama. The soil in the shortgrass type, bared as a consequence of drought, was usually repopulated with weedy species such as little barley *(Hordeum pusillum)*, peppergrass *(Lepidium densiflorum)*, sticktight *(Lappula heterosperma)*, Russian thistle *(Salsola pestifer)*, lamb's quarters *(Chenopodium album)*, and many others. These weeds were often detrimental to the recovery of buffalo grass because of their shade and also because of their rapid absorption of water (Fig. 28). By the end of the drought, despite rapid and repeated local recovery, buffalo grass had lost much more than the more stable blue grama. Of the present (1940) cover of short grasses throughout this arid western region, buffalo grass constitutes probably not more than one half as much as does blue grama.

Variations in the cover of short grass with the drier and less dry years have been fully presented by Albertson and Weaver (1942), and also in connection with an extensive survey of hundreds of square miles of western range (Weaver and Albertson 1939). The most reduced cover in the short-grass type occurred in 1936 (5 and 2.5 percent in moderately grazed and overgrazed ranges, respectively) and in 1939 in protected ranges, where it was reduced to 22 percent. There was some increase, due largely to the spread of buffalo grass, until 1940 when there was again a sharp decrease. This was followed by rapid gains in 1941 when the good rains came.

FIG. 28. Detail of dense growth of little barley *(Hordeum pusillum)* at Phillipsburg, Kan., on July 18, 1941. The grass, which has seeded, overtops scattered mats of buffalo grass and blue grama.

PANICUM VIRGATUM

Tall panic grass was most commonly found growing in the big bluestem habitat in clumps from one to several feet in diameter. It occurred less frequently in smaller bunches among other grasses in the little bluestem type on the hillsides. This deeply rooted grass suffered comparatively small losses. During the less severe years of drought the flower heads were borne close to the ground but during the driest ones none developed.

AGROPYRON SMITHII

Western wheat grass was widely distributed throughout the mixed prairie in 1932. It occurred in greatest abundance in the deepest soil on the ecotone between the short-grass and little bluestem types. It also comprised a considerable portion of the vegetation on the lower slopes. By 1940, it had frequently taken complete possession of large areas on the hillsides where the soil was deep enough for it to gain a foothold. Even on the lowlands where big bluestem was usually dominant, it formed an important part of the vegetation (Fig. 29). It is also

Fig. 29. Increase of western wheat grass (light color) over lower slopes and in ravines at Hays, Kan., as it appeared in the spring of 1939.

found in buffalo wallows scattered throughout the short-grass habitat, but here the living rhizomes remained dormant during several years with little or no growth above ground.

Other Perennial Grasses

Sand dropseed *(Sporobolus cryptandrus)* is perhaps the most widely spread and important of the minor grasses. Under normal conditions of precipitation it was usually restricted to sandy soil, but with the destruction of climax vegetation by drought and the appearance of bare areas, this species spread rapidly on hard lands. It is not uncommonly a local dominant (Fig. 30).

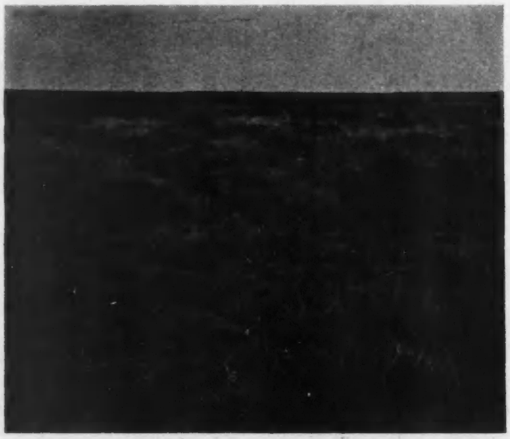

Fig. 30. Russian thistles (dark clumps) and sand dropseed (light) in a range near Marienthal, Kan., at the close of the drought.

Squirreltail *(Sitanion hystrix)* was widely distributed but found most abundantly where the cover of short grasses was more or less interrupted as along transitional areas into mid-grass types. Its root system is shallow and it perished in the early years of drought. By 1940 it was rarely seen.

June grass *(Koeleria cristata)* occupied a position very similar to that of squirreltail and suffered the same fate. In fact, none could be found at the close of the drought period. *Carex praegracilis,* frequently found in small openings in the short-grass cover, has likewise disappeared.

The occurence of hairy grama *(Bouteloua hirsuta)* and hairy dropseed *(Sporobolus pilosus)* is rather definitely limited, in western Kansas, to abrupt slopes in the little bluestem type where rocks outcropped. Both species maintained their abundance or gained slightly and are now the most important grasses in their restricted habitats.

Indian grass *(Sorghastrum nutans)* and wild rye grasses *(Elymus canadensis* and *E. virginicus)* were usually limited to local areas in the big bluestem habitat. Occasionally, however, small clumps were found ranging well up the hillsides. In these more xeric locations they succumbed and they have not increased even on the lowlands.

Dropseed *(Sporobolus asper* var. *hookeri)* was limited to small, local patches on the lower hillsides and upper ravines previous to the drought. With decrease in big bluestem, however, it made rapid gains and now has full possession of many rather large areas on lowlands. Plains muhly *(Muhlenbergia cuspidata)* is of little importance. It is usually limited to sandy knolls or rocky outcrops.

Tumblegrass *(Schedonnardus paniculatus)* and windmill grass *(Chloris verticillata)* were commonly found in disturbed places where they sometimes formed the major part of the cover. Both, however, were unable to survive the drought and were early replaced by sand dropseed. They are now found only occasionally in the short-grass type where the cover has been materially reduced by drought and accumulations of dust.

Annual Grasses

Before the dry years the only annual grasses of much importance in the mixed prairie and short-grass disclimax were little barley *(Hordeum pusillum)* and six-weeks fescue *(Festuca octoflora)*. Even little barley was not abundant. As the soil became bared of vegetation, however, it increased greatly and often produced a crop of forage of one to two tons per acre (Fig. 28). Six-weeks fescue, on the other hand, suffered a high rate of mortality and at the close of the drought was seen infrequently.

Other weedy annual grasses that invaded open places were downy brome *(Bromus tectorum)*, chess *(B. secalinus)*, *B. japonicus,* witch grass *(Panicum capillare)*, and ill-scented love grass *(Eragrostis cilianensis)*. Under most adverse conditions, where the native cover was almost entirely destroyed, these grasses produced a new but often patchy cover annually (Fig. 31).

Studies on the Composition of Plant Cover

The amount and composition of basal cover were ascertained at the end of the drought. Data are from more than 100 permanent meter quadrats at Hays, Kansas, and territory extending 200 miles southwestward. They were located not only in the short-grass type but also in both big bluestem and little bluestem habitats and in the transition between the latter and the short grasses (Table 2).

FIG. 31. Downy bromegrass (light) alternating with patches of western wheat grass (dark) on June 25, 1941. Scattered, relic native grasses are completely hidden by the bromegrass.

TABLE 2. Percentage composition of the basal cover of various species of four chief communities of mixed prairie vegetation before and after the great drought.

Species	Short-grass type		Ecotone		Little bluestem type		Big bluestem type	
	1932	1940	1932	1940	1932	1940	1932	1940
Bouteloua gracilis	48.5	59.0	43.0	66.0	8.0	31.0	3.0	12.0
Buchloe dactyloides	47.5	35.0	42.0	30.0	0.5	6.0	2.0	20.0
Aristida purpurea and *A. longiseta*	1.5	0.0	1.0	0.0	2.0	1.0	....	....
Sporobolus cryptandrus	0.0	3.5	....	....	7.0	7.0	....	....
Sitanion hystrix	0.5	0.0	1.0	0.5	....	....	....	....
Schedonnardus paniculatus	0.0	1.0	....	....	....	....	....	....
Andropogon scoparius	1.0	0.0	5.0	0.0	45.0	1.0	1.0	0.0
Bouteloua curtipendula	....	....	5.0	1.0	17.0	42.0	5.0	15.0
Andropogon furcatus	....	....	1.5	0.0	17.0	4.0	76.0	15.0
Sporobolus pilosus	....	....	0.1	1.0	1.0	2.0	....	....
Bouteloua hirsuta	....	....	....	....	2.0	5.0	....	....
Panicum virgatum	....	....	....	....	....	....	2.0	2.0
Agropyron smithii	....	....	....	....	....	....	4.0	20.0
Sorghastrum nutans	....	....	....	....	....	....	2.0	0.0
Elymus virginicus	....	....	....	....	....	....	2.0	1.0
Sporobolus asper var. *hookeri*	....	....	....	....	....	....	2.0	13.0
Total	99.0	98.5	98.6	98.5	99.5	99.0	99.0	98.0

In the short-grass type, *Bouteloua gracilis* constituted 48.5 percent of the total vegetation (that is, the 90 percent of short-grass cover) in 1932. In 1940, it composed 59 percent of the greatly reduced plant cover (that is, about 20 per cent of the predrought amount). The cause for the increase in relative abundance—not total amount—of *Bouteloua gracilis* was a decrease in the abundance of *Buchloe dactyloides.* Conversely, buffalo grass composed 47.5 percent of the original cover but only 35 percent of the greatly reduced one at the end of the drought. The species of Aristida, *Sitanion hystrix,* and *Andropogon scoparius* had disappeared completely. *Sporobolus cryptandrus* and *Schedonnardus paniculatus,* although never important in this type, were found only at the close of the drought.

When the drought ended, about 1940, the highly drought-resistant blue grama composed approximately two thirds of the vegetation in the short-grass type. Buffalo grass alone constituted approximately one third; other grasses and forbs were very sparsely represented. But this relationship changed quickly owing to the rapid vegetative spread of buffalo grass. This is well illustrated by another group of 25 short-grass quadrats at Hays, Kansas. In 1939, the basal cover provided by grama grass and buffalo grass was 11.6 and 10.5 percent, respectively. The next year the percentages were 10.8 and 8.1. But in 1941 buffalo grass had gained greatly, the percentages of cover in the same sequence being 15.7 and 36.

In the ecotone, the behavior of *Bouteloua gracilis* and *Buchloe dactyloides* was similar to that in the short-grass type. Blue grama increased in percentage from 43 to 66; a decrease from 42 to 30 was ascertained for buffalo grass. Five mid- and tall grasses, found in amounts of 5 percent or less, suffered losses (Table 2).

In the *Andropogon scoparius* type, the dominant decreased from 45 to 1 percent. Species of Aristida and *Andropogon furcatus* suffered losses, the bluestem decreasing from 17 to 4 percent. The more xeric species increased. *Bouteloua gracilis* increased from 8 percent to 31, *B. curtipendula* from 17 to 42 percent, but *Buchloe dactyloides* from only 0.5 percent to 6 (Table 2).

In the *Andropogon furcatus* type, the dominant decreased from 76 percent to 15, and *A. scoparius* from 1 percent to 0. *Sorghastrum nutans* and *Elymus virginicus* occurred in small amounts but both decreased; the 2 percent of *Panicum virgatum* remained unchanged. All other species increased, *Bouteloua curtipendula* threefold, *Agropyron smithii* from 4 to 20 percent, and *Sporobolus asper* var. *hookeri* from 2 to 13 percent. Even the short grasses now received enough light to spread among the greatly thinned and dwarfed taller species. *Bouteloua gracilis* increased from 3 to 12 percent but *Buchloe dactyloides* from 2 to 20.

Considering the whole portion of the mixed prairie and its short-grass disclimax that were studied, the grasses may be divided into three groups. Species in each group are arranged as nearly as possible in order of decreasing importance. This 1940 distribution of grasses, including certain weedy species of the subsere, is as follows:

Short-grass Type

Species of Major Abundance

Bouteloua gracilis *Buchloe dactyloides*

Species of Intermediate Abundance

Bouteloua curtipendula *Agropyron smithii*
Sporobolus cryptandrus

Species of Minor Abundance

Aristida spp. *Chloris verticillata*
Schedonnardus paniculatus *Sitanion hystrix*
Muhlenbergia cuspidata

Other Types

Species of Major Abundance

Bouteloua curtipendula	*Andropogon furcatus*
Agropyron smithii	*Sporobolus asper* var. *hookeri*
Bouteloua gracilis	
Buchloe dactyloides	

Species of Intermediate Abundance

Panicum virgatum	*Bouteloua hirsuta*
Sporobolus cryptandrus	*Sporobolus pilosus*

Species of Minor Abundance

Andropogon scoparius	*Sitanion hystrix*
Aristida spp.	*Schedonnardus paniculatus*
Sorghastrum nutans	*Muhlenbergia cuspidata*
Elymus canadensis	*Koeleria cristata*
Elymus virginicus	

RESURVEY OF FORBS

Forbs constitute an important part of prairie vegetation. They furnish the seasonal aspects and contribute largely to the layering in grassland both above and below ground. Nearly all of the legumes are valuable as forage and they contribute considerable amounts to the total yield. The lead plant *(Amorpha canescens)* alone supplied 200 pounds per acre of air-dry forage from a prairie in western Iowa when the vegetation was clipped near the soil surface four times during the growing season (Fig. 32). The list of native forbs that are regularly eaten by stock and hence decrease under close grazing is a long one; the list of those that are grazed but little and increase in pasture is much shorter (Weaver and Hansen 1941). Undoubtedly forbs provide a valuable variety in the diet of livestock. Native forbs, in conjunction with various kinds of grasses, have long been employed as indicators of the degree of severity of grazing. When supplemented by a knowledge of the presence of invading species and conditions of the surface soil, they afford a reliable index of the degree of degeneration from prairie and of the productivity of range land. On these bases, midwestern native pastures have been classified into four distinct stages of deterioration.

Fig. 32. A thick stand of prairie shoestring or lead plant in ungrazed prairie near Guthrie Center, Ia., on June 14, 1937.

Forbs have long been used as indicators of mesophytism in types of grassland, since most of them thrive on the water supply that is available in excess of the needs of the grasses. More than half of the upland, true-prairie forbs are rooted at greater depths than 5 to 6 feet and thus beyond the depths of usual root penetration of upland grasses. In mixed prairie, although still abundant, they were always fewer. Here, too, soil moisture is less plentiful and deep soils constantly dry. Small wonder that, with the oncoming of several years of greatly reduced precipitation and severe atmospheric drought, the toll of forbs was great and losses especially pronounced in the mixed prairie and short-grass plains disclimax.

The losses of forbs have been studied throughout the drought. Since many prairies were visited at regular intervals each year and hundreds of quadrats recharted annually, a comprehensive record of the actual weakening and death of forbs was obtained. These studies show that the decrease in numbers was not gradual but sporadic, corresponding with severity of drought. Deeply rooted plants such as *Rosa arkansana, Amorpha canescens,* and *Kuhnia glutinosa* have frequently held out against drought and competition with western wheat grass until the last two or three years. Some still persist. In many prairies they are about the only forbs that remain except drought-evading species which grow only in spring. Quite in contrast, *Antennaria campestris, Fragaria virginiana,* and many other shallowly rooted plants were nearly all killed at the first great impact of the drought in 1934 and have never reappeared, except a few in the most favorable sites. Others like *Helianthus rigidus* and *Echinacea pallida* lingered a second year; plants of most species persisted a little longer and were continuously depleted in numbers with recurring periods of drought.

By 1940 most species of forbs had decreased greatly, some almost to the point of extinction, as a consequence of the continued recurrence of dry years. This pertains to those that root deeply as well as to those of moderate and shallower rooting habits. Loss of legumes was especially noticeable. Little loss occurred in Iowa; it was very heavy in eastern Nebraska and Kansas, and westward very few species were found during the later years of the drought. Only a few reports of their decreases have been published and these have been in connection with deterioration of the grasses (Weaver, Stoddart, and Noll 1935; Weaver and Albertson 1939; Weaver 1942).

Nature and Causes of Losses

During the first great impact of drought, large numbers of forbs succumbed with the grasses. Others

suffered midsummer death above ground only. These recovered the next year only to undergo severe drying in 1936. There is some evidence that certain species, persisting on subsoil moisture at depths below 4 to 5 feet, extended their roots even more deeply. But even at the beginning of drought, available soil moisture below the solum, although extending deeply, was small in amount. Throughout the years of drought, precipitation did not augment this supply and even deeply rooted plants were forced to depend upon water largely from current precipitation. Thus, as years of severe drought (1934, 1936, 1937, 1939) alternated with those of more moderate soil moisture deficiencies, loss of forbs was progressive. In 1939 it was stated that "most species of forbs . . . have gradually succumbed to the continued drought, until they are only one-half to one-third of their former abundance" (Weaver and Albertson 1939). Since that time there have been further marked decreases in a weakened plant population.

Drought occurred during various periods of the year—early spring, late spring, midsummer, and late summer. Wilting, drying, and more or less complete defoliation of tops by grasshoppers were common phenomena later in the drought cycle among even the most deeply rooted species. Dwarfness in stature was characteristic of the more drought-resistant species which continued to grow slowly, even if intermittently. Lack of debris on the soil with little or no cover of grasses and lack of the usual shade accentuated the drought. Failure to complete vegetative growth or to blossom or ripen seed was usual. Seasonal aspects, if any, were poorly marked, compared with the former wealth of flowers. This resulted finally in a dearth of viable seed which, in conjunction with a general environment unfavorable to seedling establishment, resulted in few seedlings. Seedlings were not found except rarely in the hundreds of permanent quadrats that have been carefully examined year by year (Weaver and Hansen 1941a; Albertson and Weaver 1942). Thus little or no replacement of the forb population occurred over a period of 6 or 7 years.

Development of only a few stems from crowns of perennial species that normally supported many revealed at once the severe environment and the weakened condition of the vegetation. Often the forbs were robbed of the meager water supply in spring by the growth of a host of annual grasses, some of which were native, as *Festuca octoflora,* but mostly ruderals such as various species of bromegrass and little barley. Although weedy forbs are still plentiful in mixed prairie, eastward the scourge of peppergrass *(Lepidium densiflorum),* horseweed *(Leptilon canadense),* and, more locally, goat's beard *(Tragopogon pratensis),* so common until 1938, has vanished.

In many prairies, especially westward, death by mechanical injury from blowing dust overtook aboveground parts, or both forbs and grasses were smothered under a blanket of dust a few to many inches thick. Where denudation eastward resulted from extreme drought and only deeply rooted forbs survived, these sometimes died because of invasion of needle grass and more regularly by a similar invasion of western wheat grass.

During the last 3 years many drought-bared areas had been reclaimed by needle grass. The rather small, uniform bunches so completely utilized all available water in their early growth that all relic forbs had been killed and rarely was any plant to be found other than the grass. An exception was the drought-resistant, many-flowered aster *(Aster multiflorus).* The grass in repopulating the area revealed complete dominance on hillsides where a few years before a wealth of forbs was growing as lower, middle, and upper layers with little bluestem. Side-oats grama and blue grama often occurred in similar, relatively new stands without accompanying forbs. The very detrimental role of the dense sod of wheat grass has been illustrated elsewhere.

A few species of native forbs profited by the death of their competitors. Chief among these were *Aster multiflorus, Solidago glaberrima, Erigeron ramosus,* and the annuals, *Specularia perfoliata,* and *Silene antirrhina.* Increase of the annuals was marked during the first years of drought only and Erigeron has fluctuated greatly from year to year. The two perennials, both propagating by means of rhizomes, although not so abundant at the end of the drought as in 1937, still occur in true prairie in numbers greatly exceeding the predrought normal.

Another group of species, practically all with rootstalks or other storage organs, has increased, some to a remarkably great extent.

COMPARATIVE NUMBER OF LONG-LIVED SPECIES

Complete lists of the species of native forbs found at each of three groups of prairie stations were made during the years 1930-1932 and thus before the drought (Weaver and Fitzpatrick 1934). Oakland and Glenwood, Iowa, were not included; hence data from two other typical southwestern Iowa prairies were used. Similar lists were made in 1938 and again in 1940. These lists, with the annual forbs omitted, provide a basis for comparing the destructive effect of the drought. They tell nothing, however, of the abundance of species, but merely the kinds that occurred, even if represented by a single relic plant (Table 3).

TABLE 3. Number of species of long-lived native forbs found at the several stations in true prairie before, during, and at the end of the drought.

Stations	1930	1938	1940	Stations	1930	1938	1940	Stations	1930	1938	1940
Corning	82	..	80	Lincoln	52	44	41	Carleton	35	22	19
Guthrie Center	88	..	87	Hebron	49	41	35	Clay Center	35	32	24
Anita	84	..	80	Belleville	48	31	46[3]	Montrose	44	23	21
Average	85	..	82		50	39	41		38	26	21

[3] This prairie was severely damaged early in the drought but maintained one excellent large area of bluestems and accompanying forbs.

Although the prairies varied somewhat in size, at least one in each group contained 80 or more acres, and the smallest one (Clay Center) possessed as many species as the others in its group. Average mean annual precipitation decreased from 32.4 inches in Iowa to 25.9 inches at the Carleton group of stations. Accompanying this reduction in precipitation was a decrease of 55 percent in average number of long-lived forbs. The percentage decrease at the Lincoln group of stations with an average precipitation of 27.1 inches was 41. These are the predrought figures. Losses during drought were progressive, except at Belleville. In 1940, only half as many species occurred at the Lincoln group as in Iowa, and at the stations where forbs were overrun by western wheat grass, only about one fourth of the number occurring in Iowa was found.

Relative Size Before and During Drought

The same species of forb decreased considerably in stature even before the drought as its habitat became drier westward. The native bluestem grasses also have been shown to be dwarfed in a similar manner. For example, on August 29, 1929, height of little bluestem in a series of prairies in Iowa varied from 16 to 26 inches. It was 10 to 11 inches less in a similar group of grasslands near Lincoln. On July 17 to 19, 1931, big bluestem at a group of western Iowa stations varied from 18 to 40 inches in average height, but a week later in prairies southwest of Lincoln the height was only 15 to 18 inches. Stature of forbs varied somewhat in proportion to the grasses.

During and near the end of the dry years, differences in stature were greatly increased, since drought was either absent or not severe in the Iowa prairies. Hundreds of measurements have been made but only a few will be used to illustrate a general condition. *Kuhnia glutinosa* was 30 to 42 inches tall in Iowa, 12 to 14 inches at the Lincoln stations, but only 4 to 10 in the wheat grass group (Fig. 33). Similar data for *Rosa arkansana* are 24 to 36, 14 to 22, and 5 to 7 inches, respectively. Those for *Amorpha canescens* are 19, 7, and 5 inches. At the Iowa stations a tall layer of forbs was always conspicuous above the bluestem grasses (Figs. 34, 35, and 36). *Helianthus rigidus*, for example, was 40 to 60 inches tall with 4 to 6 flower heads per stalk. The few relics at Lincoln were only 12 to 18 inches high and had a single, small, terminal flower. At some bluestem stations *Amorpha canescens* was sometimes the sole species visible above the dwarfed and dried bluestems. A stand of western wheat grass even 14 inches tall obscured the presence of all the widely spaced, dwarfed forbs.

Decrease in Numbers

The relative abundance and ecological importance of each species of forb were studied and closely estimated. The various species in a prairie were placed in one of each of five classes or ranks, ranging from the chief society formers to plants of infrequent or rare occurrence. The relative ranking was determined only after carefully studying the abundance, size, duration, density, gregariousness, and basal and foliage cover of each species (cf. Weaver and Fitzpatrick, The Prairie). The rankings in decreasing importance are from 1 to 5. Since these lists were made before the drought, again in 1938, and near the end of the drought, changes resulting from desiccation are clearly revealed. Changes of importance in 34 species are shown for 6 stations in Table 4; the Iowa stations are not included since little change occurred there.

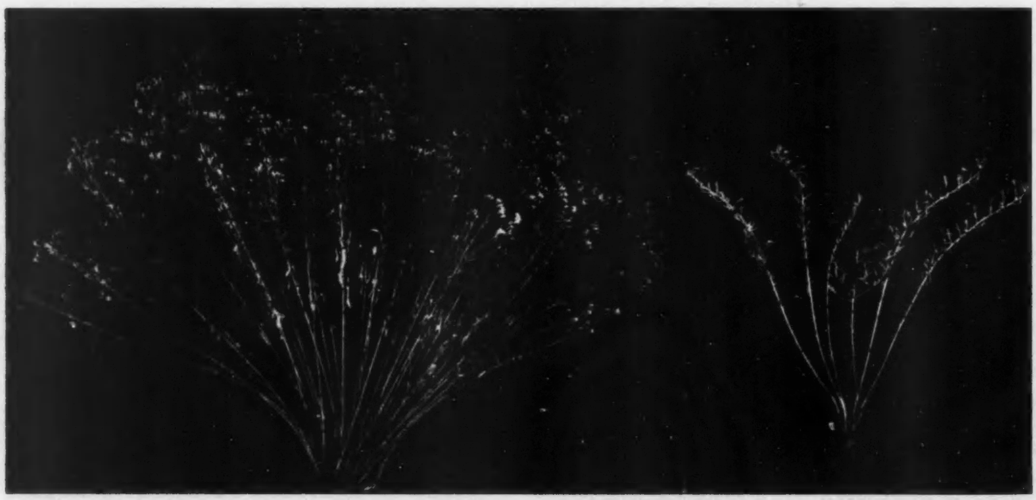

Fig. 33. False prairie boneset *(Kuhnia glutinosa)* from prairie at Oakland, Ia., and a plant of the same species from Hays, Kan. The first, with 39 stems, is about 42 inches tall; the drought-stricken plant, with stems reduced to 5, is only 15 inches high.

Examination of table 4 shows that *Oxalis violacea* alone increased at all stations. Eleven species (designated by a superior 1) remained about the same. Nineteen species (superior 2) decreased considerably or at least at 5 of the 6 stations. *Aster multiflorus* (including *A. batesii*) decreased at all but two stations. Two others (superior 3) entirely disappeared. Losses were greatest in the wheat grass prairies (last 3 stations with 32 species) where only 5 species (Amorpha, Kuhnia, *Liatris punctata*, Vernonia, and Cirsium) changed but little, 13 disappeared entirely, and 13 decreased or disappeared at some stations. One, *Oxalis violacea*, increased.

FIG. 34. Forbs in upland prairie at Oakland, Ia., on August 5. The tick-trefoil *(Meibomia illinoensis)* is about 5 feet high and the blazing star *(Liatris scariosa)* 44 inches.

ABUNDANCE IN 1940

The species of native, long-lived forbs found at the end of the drought at the several prairie stations are given with their ratings in Table 5. The first section includes 59 species found at the Iowa stations only. They did not occur at any of the other 6 stations in true prairie. All but 6 species ranked as rare (5), infrequent (4), or common (3). *Coreopsis palmata, Corylus americana, Euphorbia corollata,* and *Liatris pychnostachya* alone ranked as societies

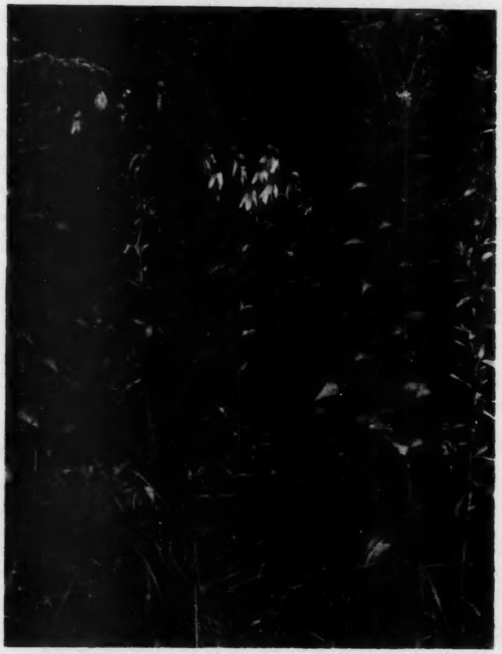

FIG. 35. Three characteristic forbs of western Iowa which on August 5 extended far above the 20-inch grass level and attained heights of 45 to 50 inches. From right to left are *Lespedeza capitata, Vernonia baldwini,* and *Lepachys pinnata.*

of the first class (1). *Corylus americana* and *Salix humilis* are shrubs, but under annual mowing their growth simulates that of coarse forbs. In general, this list represents a group of the more mesic prairie forbs.

The second section includes a group of 36 species, mostly of more xeric habit, which were found in Iowa or Nebraska-Kansas bluestem prairies only. Here the

FIG. 36. Portion of a society of *Helianthus rigidus* on level upland in western Iowa on August 5. The plants are over 4 feet high. Bluestems at their base have been removed.

Table 4. Most important forbs occurring at least at three of the several Nebraska-Kansas stations. Species are arranged after the lists of Weaver and Fitzpatrick in order of their general ecological importance in prairie. The rating for each species in each prairie is given for 1931, 1938, and 1940.

Species	Belleville			Crete			Valparaiso			Carleton			Clay Center			Montrose		
	1931	1938	1940	1931	1938	1940	1931	1938	1940	1931	1938	1940	1931	1938	1940	1931	1938	1940
Amorpha canescens [1]	1	2	1	1	1	3	1	1	1	2	1	1	1	1	1	1	2	2
Helianthus rigidus [2]	5	0	5	1	4	4	1	3	5									
Aster multiflorus	1	4	3	1	1	1	2	1	1	1	3	5	1	3	5	1	2	4
Antennaria campestris [2]	1	5	5	1	4	5	1	3	5	4	0	0	2	0	0	3	0	0
Erigeron ramosus [2]	1	4	4	1	2	3	1	3	1	1	0	4	1	5	3	5	5	4
Solidago glaberrima [2]	5	5	0	1	1	2	1	3	4	4	4	4	2	3	5	4	5	5
Psoralea argophylla [2]	3	0	0	3	4	5	1	5	5	3	3	4	1	3	5	1	5	4
Petalostemon candidus [2]	4	5	4	3	5	5	1	4	5	4	5	5						
Petalostemon purpureus [2]	4	5	3	3	5	5	1	4	5	4	5	5						
Solidago rigida [2]	5	5	5	3	5	0	3	5	0	4	5	0	1	0	0	5	0	0
Astragalus crassicarpus [2]	5	0	5	4	5	4	4	4	5	4	0	0	3	5	5	5	0	0
Liatris scariosa [2]				5	0	5	3	5	5	5	0	0						
Rosa arkansana [2]	3	3	4	2	3	4	5	5	4	4	1	2				4	3	3
Kuhnia glutinosa [1]	3	4	5	5	5	0	4	3	3	5	3	3	3	5	5	4	3	2
Psoralea floribunda [1]				1	1	1	5	5	5							5	0	0
Sisyrinchium angustifolium [3]	1	0	0	4	0	0				4	0	0	2	0	0			
Liatris punctata [1]	2	3	5				3	4	3	5	5	4	5	5	4	4	3	3
Meibomia illinoensis [2]	5	5	0	4	4	5	5	0	5									
Artemisia gnaphalodes [2]	1	4	4	4	4	4	3	4	4	4	5	0	1	3	4	4	4	0
Solidago rigidiuscula [3]	2	0	0	5	0	0	3	0	0	4	0	0				1	0	0
Achillea occidentalis [2]	4	0	4	5	5	5	4	0	0	4	0	0	5	0	0			
Senecio plattensis [2]	5	0	5	5	2	5	5	4	0	2	0	0	2	0	0			
Lepachys columnifera [2]			4	5	0	0	4	0	0	5	5	0				4	0	0
Callirhoe alcaeoides [1]	5	4	5							1	4	5	4	4	5	4	4	4
Physalis lanceolata [2]	4	0	0	4	5	5	4	0	0	5	5	0	5	5	0	5	0	0
Lithospermum linearifolium [1]	5	5	5			5		5	4			5	5	5	0	5	5	0
Hieracium longipilum [2]	5	0	0	5	5	5										4	0	0
Delphinium virescens [1]			5	5	4	5						5	5	0	0	5	4	0
Meriolix serrulata [1]	4	5	3				4	5	5	5	5	5	5	5	5	5	0	0
Gentiana puberula [1]				5	5	5	5	5	5				5	0	0			
Glycyrrhiza lepidota [2]	4	5	5	4	4	5	3	5	5							4	0	0
Vernonia baldwini [1]	4	4	5	4	4	5	3	5	4	5	5	5		5	5	4	5	4
Cirsium undulatum [1]	4	5	5			5				5	0	0	4	4	4	4	0	4
Oxalis violacea			2	4	2	3			5	4	3	2		1	3	4	5	1

ranking is variable, but the occurrence is predominantly infrequent (4) or rare (5).

A final list of 36 xeric species was found at the western wheat grass prairies or *(Psoralea floribunda* and *Tradescantia bracteata)* at the Nebraska little bluestem stations only. Fourteen species were found only at the two westerly station groups. Four species, all very xeric—*Allionia linearis, Gaura coccinea, Lygodesmia juncea,* and *Malvastrum coccineum*—were found at the wheat grass stations only.

Average number of species at the three station groups from east to west was 85, 40, and 21, respectively. The scarcity of most species is shown by the fact that 75 percent of the listings were in classes 4 or 5 and only 12 percent in classes 1 and 2.

The forbs at the three mixed-prairie stations and twelve others westward are listed in Table 6. This group of 17 species includes all the long-lived forbs found. *Kuhnia glutinosa, Aster multiflorus,* and *Liatris punctata* occurred at all of the grassland station groups from Iowa westward. The species from *Allionia linearis* to *Solidago mollis* inclusive, except *Psoralea tenuiflora,* occurred at some wheat grass stations as well as in mixed prairie, but like the five remaining species, which except Sideranthus were found in mixed prairie only, they are distinctly more western in distribution and more xeric than some of the preceding. Only 1 or 2 species occurred at some stations and never more than 10 to 12 were found.

The lowest ebb of vegetation at these stations was reached in spring and early summer of 1940, following the great drought which extended through the fall and winter of 1939. The ten most drought-resistant species (excepting the cacti) are each preceded by an asterisk. All could be found in 1938-1939 in nearly every range, not abundantly and always scattered, especially after some searching. But after the drought of 1939, only Malvastrum, Kuhnia, Psoralea, and Cirsium could be found after prolonged searching in favored spots; the rest were seen rarely. This explains the overwhelming number of low ratings (4 and 5) and, except for cacti, the rare occurrence of any species in abundance at any station.

The cause of drought resistance of these 10 species has not been studied specifically on a physiological basis. It may be found to be inherent in the protoplasm. The following observations, however, are pertinent. Nearly all of these species are deeply rooted and thus may utilize all available water throughout the soil to the depth of water infiltration.

TABLE 5. Species and rating of forbs occurring at the end of the drought in upland bluestem prairies of Iowa, upland bluestem prairies of eastern Nebraska and Kansas, and in wheat grass prairies in eastern Nebraska and north-central Kansas.

1. SPECIES LISTED IN IOWA ONLY

Species	Guthrie Center	Corning
Anemone cylindrica	4	5
Antennaria plantaginifolia	5	5
Apocynum cannabinum	5	4
Apocynum sibiricum	3	5
Asclepias pumila	5	..
Asclepias sullivantii	..	5
Asclepias verticillata	4	4
Aster laevis	5	5
Aster sagittifolius	3	3
Aster sericeus	4	5
Astragalus carolinianus	5	..
Baptisia leucantha	4	5
Chamaecrista fasciculata	4	5
Comandra umbellata	2	4
Coreopsis palmata	1	1
Corylus americana	1	..
Drymocallis agrimonioides	4	3
Equisetum arvense	5	5
Eryngium yuccifolium	3	3
Eupatorium perfoliatum	5	..
Euphorbia corollata	1	1
Euthamia graminifolia	5	4
Fragaria virginiana	5	5
Galium tinctorium	5	5
Gaura parviflora	..	5
Geum album	5	..
Habenaria leucophaea	5	..
Helianthus grosseserratus	4	4
Heuchera americana	4	3
Hieracium scabrum	5	..
Houstonia angustifolia	..	4
Hypoxis hirsuta	5	..
Lepachys pinnata	5	4
Leptandra virginica	4	4
Liatris pychnostachya	2	1
Liatris squarrosa	4	2
Lithospermum gmelini	4	5
Meibomia canadensis	5	5
Onosmodium hispidissimum	5	..
Pedicularis canadensis	4	4
Phlox pilosa	4	4
Physalis heterophylla	5	5
Physalis virginiana	5	..
Potentilla monspeliensis	..	5
Prunella vulgaris	5	..
Pycnanthemum flexuosum	4	4
Salix humilis	4	4
Senecio aureus	4	4
Sieversia ciliata	..	5
Silphium laciniatum	4	3
Solidago canadensis	4	4
Solidago rigidiuscula	..	3
Steironema ciliatum	5	5
Tradescantia occidentalis	..	5
Vernonia fasciculata	..	4
Viola papilionacea	4	4
Viola pedata	3	..
Viola pedatifida	4	5
Zizia aurea	5	3

2. SPECIES LISTED IN BLUESTEM PRAIRIES ONLY

Species	Guthrie Center	Corning	Valparaiso	Crete	Belleville	Carleton	Clay Center	Montrose
Achillea occidentalis	5	2	..	5	4	..	..	..
Allium nuttallii	..	..	..	..	4	..	..	..
Antennaria campestris	3	1	5	5	5	..	..	..
Apocynum androsaemifolium	..	..	..	5	..	..	..	..
Asclepias amplexicaulis	..	..	..	..	5	..	..	..
Asclepias tuberosa	5	4	..	5	..	..	..	..
Aster oblongifolius	..	..	5	..	..	..	..	..
Baptisia leucophaea	4	4	..	5	..	..	..	..
Blephariglottis leucophaea	..	..	..	..	2	..	..	..
Ceanothus pubescens	1	1	5	5	..	..	..	..
Cogswellia daucifolia	..	..	5	..	..	..	..	..
Cogswellia orientalis	..	..	..	..	4	..	..	..
Echinacea pallida	4	1	3	5	..	..	..	..
Equisetum laevigatum	4	5	5	5	..	..	..	..
Erythronium mesochoreum	..	..	4	..	..	..	..	..
Gentiana puberula	5	4	5	5	..	..	..	..
Glycyrrhiza lepidota	4	5	5	5	5	..	..	..
Hieracium longipilum	2	3	..	5	..	..	..	..
Helianthus maximiliani	5	..	..	..	5	..	..	..
Helianthus rigidus	1	2	5	4	5	..	..	..
Heliopsis scabra	4	4	3	..	..	..	..	..
Lepachys columnifera	4	3	..	..	4	..	..	..
Lespedeza capitata	5	5	..	..	5	..	..	..
Liatris scariosa	3	3	5	5	..	..	..	..
Meibomia illinoensis	4	5	5	5	..	..	..	..
Mesadenia tuberosa	5	5	..	5	..	..	..	..
Nabalus asper	..	..	..	5	..	..	..	..
Onagra biennis	..	..	..	5	..	..	..	..
Opuntia humifusa	..	..	..	..	3	..	..	..
Petalostemon purpureus	5	4	5	5	4	..	..	..
Physalis lanceolata	..	..	..	5	..	..	..	..
Rhus rydbergii	4	3	3	..	4	..	..	..
Silphium integrifolium	2	3	5	..	..	..	..	..
Sisyrinchium angustifolium	3	4	..	..	..	..	..	..
Solidago altissima	..	4	..	5	5	..	..	..
Solidago rigida	4	4	..	..	5	..	..	..

3. SPECIES FOUND IN WHEAT GRASS PRAIRIES

Species	Guthrie Center	Corning	Valparaiso	Crete	Belleville	Carleton	Clay Center	Montrose
Acerates angustifolia	..	..	..	..	4	5	5	4
Acerates viridiflora	..	..	4	5	4	..	5	..
Agoseris cuspidata	..	..	..	..	4	..	..	5
Allionia linearis	..	..	..	..	..	..	5	5
Allium mutabile	..	..	..	5	4	5	..	..
Amorpha canescens	1	2	1	3	1	1	1	2
Anemone caroliniana	..	..	..	..	1	3	2	1
Artemisia gnaphalodes	3	4	4	4	4	..	4	..
Asclepiodora decumbens	..	..	..	..	4	..	5	..
Aster multiflorus	4	1	1	1	3	5	5	4
Astragalus crassicarpus	5	..	5	4	5	..	5	..
Callirhoe alcaeoides	..	..	..	..	5	5	5	4
Cirsium undulatum	..	..	..	5	5	..	4	4
Delphinium virescens	5	4	..	5	5	5	..	..
Erigeron ramosus	4	1	1	3	4	4	3	4
Gaura coccinea	..	..	..	..	..	..	..	5
Kuhnia glutinosa	3	4	3	..	5	3	5	2
Liatris punctata	..	3	3	..	5	4	4	3
Lithospermum linearifolium	..	..	4	5	5	5	..	..
Lygodesmia juncea	..	..	..	..	..	..	3	..
Malvastrum coccineum	..	..	..	..	..	..	3	5
Meriolix serrulata	..	..	5	..	3	5	5	..
Oxalis violacea	5	..	5	3	2	2	3	1
Petalostemon candidus	4	2	5	5	3	5	..	..
Psoralea argophylla	4	4	4	5	..	4	5	4
Psoralea esculenta	5	..	5	..	5	..	5	..
Psoralea floribunda	..	..	5	1	..	..	..	..
Rosa arkansana	3	4	4	4	4	2	..	3
Salvia pitcheri	..	..	5	5	5	..	..	4
Senecio plattensis	..	4	..	5	5	..	5	..
Sideranthus spinulosus	..	..	..	..	5	..	..	5
Solidago glaberrima	..	4	4	2	..	4	5	5
Solidago mollis	..	..	..	..	5	..	2	1
Tradescantia bracteata	..	..	..	5	5	..	..	..
Vernonia baldwini	3	4	4	5	4	5	5	4
Vicia americana	..	..	..	5	5	5	..	..
Total number of species	87	83	35	41	45	19	24	21

Most have storage organs consisting of thick roots or underground stems which promote early growth and rapid recovery during periods with moist soil. Most of these species do not have an abundance of foliage and with the oncoming of drought, the transpiring surface is greatly reduced by loss of many

TABLE 6. Species and ratings of long-lived forbs occurring in representative ranges of 9 counties in western Kansas. Many of these ranges had not been grazed for 3 or more years, since the cover was so greatly reduced by drought or dust.

Species	Phillipsburg	Hays	Dighton	Oakley	Oakley	Scott City	Marienthal	Tribune	Tribune	Tribune	Tribune	Syracuse	Kendall	Holcomb	Kalvesta
**Kuhnia glutinosa*	5	5	5	5	5	..	..	..	..	..	..	..	..	3	3
Aster multiflorus	..	5	..	..	..	..	..	..	..	..	..	..	..	4	4
**Cirsium undulatum*	..	4	5	5	5	..	..	..	4	4	5	..	..	4	4
Lepachys columnifera	..	..	3	5	4	..	..	..	5	..	3	5	..	5	5
**Lygodesmia juncea*	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Opuntia humifusa	3	1	..	2	3	3	3	2	2	..	3	2	..	2	..
**Liatris punctata*	..	5	..	..	..	..	..	..	..	..	5	5	..	..	..
**Allionia linearis*	5	4	5	..	5	5	..	..	..	5	5	..	..	5	5
**Gaura coccinea*	4	4	4	..	5	5	..	..	..	..	4	..	..	5	4
**Malvastrum coccineum*	1	2	4	5	3	4	5	..	4	3	2	3	4	..	3
**Psoralea tenuiflora*	5	5	5	5	3	5	..	..	..	..	4	..	..	4	3
**Solidago mollis*	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Astragalus mollissimus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5
Gutierrezia sarothrae	..	..	..	..	5	5	..	..	..	..	..	..	..	5	..
Linum compactum	..	4	5	5	5	..	..	..	5	..	5	..	..	5	..
Opuntia fragilis	..	..	..	..	..	..	..	..	..	..	..	..	..	5	..
**Sideranthus spinulosus*	5	4	5	5	5	4	..	..	3	5	..	..	..	5	5

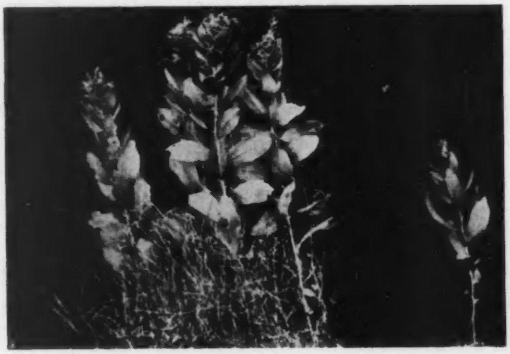

Fig. 37. *Solidago mollis* before the great drought (left). The several stems of the plant are 18 inches high. At the right is the single stemmed drought form 10 inches tall. Hays, Kan., June 30.

leaves. *Malvastrum coccineum* possesses all of these characteristics. It begins growth early, loses most of its leaves with the advent of drought, and the few that remain curl during the dry period. It is the most drought-resistant of all.

The dwarfed condition of these drought-resistant survivors was very marked. This can best be appreciated when the drought form is compared directly with plants of normal stature preceding the dry years (Figs. 37 to 40).

Fig. 38. *Liatris punctata* of normal development (left) and drought form (right). They are 21 and 11 inches tall, respectively. Hays, Kan., June 30.

Abundance in Sampling Areas

The actual abundance of forbs at each of the several stations was ascertained in 1940. This was accomplished by counting the long-lived forbs in circular areas 50 feet in diameter. Two circles in each prairie were located in typical sites representative of the prairie as a whole. Thus, plants on 3,927 square feet of soil at each station were carefully examined. Since it was impossible to distinguish individual plants of many species with branched rhizomes, and since drought-stricken plants usually had fewer stems than normal ones, the number of stems rather than the number of plants was counted. This could be done accurately by separating the circle into small sectors and examining each individually.

Fig. 39. *Psoralea tenuiflora* was perhaps the most widely spread legume of mixed prairie before the drought (left). Its usual height was about 2 feet. The single-stemmed drought form (right), taken on July 30, 1940, is only 18 inches high.

Thirty-eight species were listed at the Iowa stations only. For convenience, they are placed separately in Table 7. *Aster sericeus, Coreopsis palmata, Euphorbia corollata, Liatris squarrosa,* and *Senecio aureus* were especially abundant, the second being represented by 11,700 stems at one station.

The second section adds 18 species found in the bluestem prairies only. Species listed in section 3 are undoubtedly more xeric. In this group, three species *(Amorpha canescens, Aster multiflorus,* and *Kuhnia glutinosa)* occurred in very great numbers, but much more sparsely in wheat grass than in bluestem prairies. Number of stems of Amorpha varied from an average of 8,497 per station in Iowa to 3,904 in the bluestem prairies westward, but decreased to 610 in the wheat grass prairies. Similar numbers for Kuhnia are 1,036, 59, and 101. Aster increased in

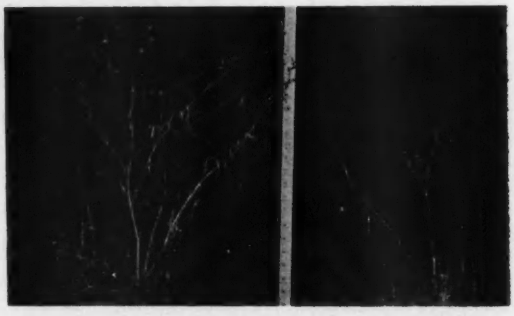

Fig. 40. Narrow-leaved four-o'clock *(Allionia linearis)* of normal size (left) and drought form (right). The one is 26 inches tall, the other 18 inches.

the western bluestem group, but practically disappeared in the wheat grass.

Average total numbers of species and stems at the Iowa stations, the Nebraska-Kansas bluestem stations, and in the wheat grass prairies were 47 and 27,875; 19 and 7,109; and 11 and 1,083, respectively. Thus the number of species at the western bluestem stations was reduced 60 percent and the number of stems 75 percent. Further reduction from the more westerly bluestem prairies to wheat grass prairies amounted to 42 percent in species but 85 percent in number of stems.

TABLE 7. Species and number of stems of forbs occurring in two circles 50 feet in diameter in bluestem prairies of Iowa, bluestem prairies of eastern Nebraska and Kansas, and in wheat grass prairies in eastern Nebraska and north-central Kansas.

1. SPECIES FOUND AT IOWA STATIONS ONLY

Species	Anita	Oakland	Species	Anita	Oakland
Anemone canadensis	14	.....	*Liatris squarrosa*	2,100	17
Anemone cylindrica	......	30	*Lithospermum gmelini*	......	11
Asclepias amplexicaulis	9	.....	*Meibomia illinoensis*	15	240
Aster azureus	121	.....	*Mesadenia tuberosa*	......	2
Aster laevis	13	655	*Onosmodium occidentale*	14	41
Aster oblongifolius	......	14	*Pedicularis canadensis*	87	.....
Aster sagittifolius	12	16	*Petalostemon purpureus*	220	61
Aster sericeus	177	1,155	*Phlox pilosa*	14	17
Ceanothus pubescens	......	735	*Physalis heterophylla*	14	16
Chamaecrista fasciculata	135	.....	*Physalis lanceolata*	195	9
Coreopsis palmata	11,700	417	*Physalis longifolia*	......	30
Drymocallis agrimonioides	......	4	*Senecio aureus*	1,350	.....
Equisetum laevigatum	203	14	*Silphium laciniatum*	27	13
Eryngium yuccifolium	19	.....	*Sisyrinchium angustifolium* and *S. campestre*	32	15
Euphorbia corollata	3,495	510	*Solidago rigidiuscula*	61	.....
Fragaria virginiana	57	63	*Viola pedata*	135	.....
Gaura parviflora	......	19	*Viola pedatifida*	641	195
Lepachys pinnata	......	7			
Lespedeza capitata	29	.....			
Liatris pychnostachya	28	.....			
Liatris scariosa	316	44			

2. SPECIES FOUND IN BLUESTEM PRAIRIES ONLY

Species	Anita	Oakland	Valparaiso	Lincoln	Belleville	Carleton	Hebron	Montrose
Acerates floridana	15	......	1	......	......	......	...	...
Achillea occidentalis	......	8	.....	2	6	......	...	...
Antennaria campestris	540	1,170	.....	21	1,076	......	...	...
Artemisia gnaphalodes	16	......	25	......	160	......	...	...
Asclepias latifolia	......	......	.....	......	8	......	...	...
Astragalus crassicarpus	......	7	.....	......	2	......	...	...
Baptisia leucophaea	......	......	.....	7	.....	......	...	...
Cirsium undulatum	14	17	.....	......	1	......	...	...
Comandra umbellata	2,100	88	1	......	1	......	...	...
Echinacea pallida	1,575	57	66	13	.....	......	...	...
Gentiana puberula	......	5	4	7	.....	......	...	...
Lepachys columnifera	16	......	.....	......	1	......	...	...
Leptoglottis nuttallii	......	......	.....	......	15	......	...	...
Lithospermum linearifolium	135	90	13	12	3	......	...	...
Meriolix serrulata	......	......	2	......	212	......	...	...
Petalostemon candidus	260	121	.....	3	12	......	...	...
Psoralea floribunda	......	......	11	31	.....	......	...	...
Senecio plattensis	......	......	.....	......	1	......	...	...

3. SPECIES FOUND IN WHEAT GRASS PRAIRIES

Species	Anita	Oakland	Valparaiso	Lincoln	Belleville	Carleton	Hebron	Montrose
Acerates angustifolia	......	......	2	1	24	1	..	1
Acerates viridiflora	......	......	......	......	12	......	...	.1
Allionia linearis	......	......	......	......	......	......	3	12
Amorpha canescens	5,370	11,625	3,923	6,140	1,648	1,320	446	65
Aster multiflorus	121	1,815	1,466	4,080	636	2	...	6
Callirhoe alcaeoides	......	......	......	......	9	2	...	...
Erigeron ramosus	101	15	7	665	30	.....	205	...
Gaura coccineum	......	......	......	......	......	......	...	32
Helianthus rigidus	178	555	.....	4	8	1	...	...
Kuhnia glutinosa	257	1,815	37	8	133	.....	28	275
Liatris punctata	32	13	74	247	380	4	...	...
Lygodesmia juncea	......	......	......	......	......	......	...	1
Opuntia humifusa	......	......	......	......	12	.....	5	1
Oxalis violacea	......	......	......	......	......	91	2	6
Psoralea argophylla	......	......	......	2	.....	11	1	2
Psoralea esculenta	30	3	2	......	49	.....	2	...
Rosa arkansana	219	6[illegible]0	1	10	.....	215	...	...
Solidago glaberrima	255	645	.....	......	......	[illegible]	4	5
Solidago mollis	......	......	......	......	......	.....	43	453
Vernonia baldwini	254	......	......	......	......	......	...	2
Total number of stems	32,721	23,029	5,635	11,253	4,439	1,650	737	862
Total number of species	48	45	16	17	24	10	10	14

Forbs at Hays and Dighton, and at 12 other stations in western Kansas where originally the vegetation was similar, are listed in Table 8. Eighteen species include all of the native forbs found (Figs. 41 and 42). The number of species per station ranged from 1 to 14 with an average representation of only 5. This occurred despite the fact the circles were twice the diameter of those used previously, and the area four times as great. The scarcity of forbs in both kinds and numbers together with their extremely dwarfed stature is impressive. One marvels,

TABLE 8. Species and number of stems of forbs occurring in two circles each 100 feet in diameter at each of several stations located in 10 counties in western Kansas. Sometimes 2 or 3 different prairies were sampled within 15 miles of one town.

Species	Hays	Dighton	Ness City	Quinter	Oakley	Oakley	Scott City	Marienthal	Tribune	Tribune	Tribune	Syracuse	Kendall	Holcomb
Allionia linearis	...	20	8	3	..	2	..	2	..	2	...	..	..	4
Ambrosia psilostachya	134	...	...	..	..	..	..	..	..	..	...	..	..	..
Aster multiflorus	...	...	...	..	..	..	..	..	..	..	...	..	..	60
Astragalus lotiflorus	...	...	...	..	..	..	..	..	..	..	...	54	..	5
Astragalus mollissimus	...	...	8	..	..	..	..	..	..	..	...	..	..	..
Cirsium undulatum	2	...	...	..	..	..	..	..	4	..	...	..	..	12
Gaura coccinea	...	36	36	..	..	..	..	..	..	..	144	..	..	12
Gutierrezia sarothrae	...	...	...	..	..	..	..	..	..	..	...	..	..	2
Kuhnia glutinosa	...	...	24	..	4	..	..	..	..	..	...	..	..	52
Lepachys columnifera	15	22	12	..	..	4	..	..	..	..	204	..	..	2
Lepachys tagetes	...	...	...	..	..	..	..	..	..	..	165	..	..	30
Linum compactum	2	...	...	..	..	2	..	..	6	..	20	..	..	4
Malvastrum coccineum	190	205	242	..	14	..	..	4	48	..	160	12	10	..
Opuntia fragilis	...	...	...	..	6	..	..	..	..	..	...	..	..	2
Opuntia humifusa	...	...	...	7	6	4	..	2	..	..	...	14	..	2
Polygonum ramosissimum	...	...	...	..	..	..	4	..	..	..	...	..	..	..
Psoralea tenuiflora	62	20	296	1	4	4	12	..	2	..	12	..	..	10
Sideranthus spinulosus	...	...	24	3	..	..	30	..	18	..	...	..	..	6

FIG. 41. Prairie near Ellis, Kan., in which non-grassy vegetation except cactus is absent. Basal cover of the short grasses is only 15 percent but the interspaces are largely occupied by little barley, peppergrass, and other weeds.

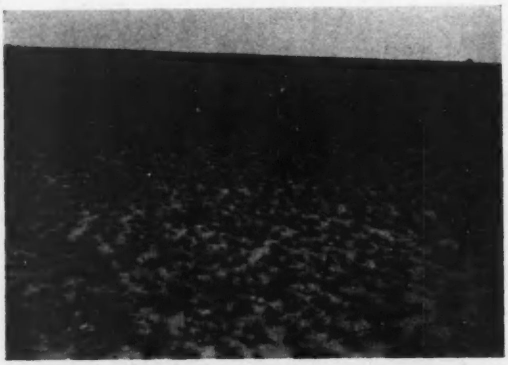

FIG. 42. General view of range near Dighton, Kan., with a characteristic open stand of grasses and almost complete absence of native forbs since the great drought.

however, not so much at the paucity of species and the thinly stretched web of life, as at the fact that any vegetation escaped the terrible drought and endured.

PREDROUGHT AND POST-DROUGHT DISTRIBUTION

The effects of the several years of drought upon the normal occurrence and abundance of the most important long-lived forbs of uplands is presented schematically in Table 9. The group that maintained approximately its predrought abundance consists of only 5 species, none of which occurred in mixed prairie. Plants that decreased in abundance constitute a list of 41 species, 8 of which range far westward. It is of interest that all maintained their usual abundance in Iowa, and all but 5 decreased in eastern Kansas and Nebraska. Among the 11 species ranging into mixed prairie also, 4 decreased and 7 disappeared. Only one species of this group, *Astragalus crassicarpus*, persisted, but in numbers greatly decreased, in the plains disclimax.

Of species mostly of mixed prairie and short-grass plains disclimax, 28 are listed. Three persisted in normal numbers—two drought-escaping species of

TABLE 9. Most important species of forbs of uplands, other than annuals, and exclusive of deep, moist ravines or of species confined to rocky outcrops, sand, or other local habitats. General predrought distribution is shown by light line. Present distribution in approximately normal numbers is shown by heavy line. A broken line indicates presence in decreased abundance, and plus signs signify a great increase in abundance. Where no line occurs other than the light one, the plants have disappeared.

Species	Western Iowa	Eastern Kan. and Neb.[1]	Mixed Prairie[2]	Plains Disclimax[3]
Species that maintained approximately their predrought abundance				
Callirhoe alcaeoides	——— ━━━	——— ━━━		
Coreopsis palmata	——— ━━━	— ━		
Equisetum laevigatum	——— ━━━	——— ━━━		
Euphorbia corollata	——— ━━━	— ━		
Gentiana puberula	——— ━━━	——— ━━━		
Species that decreased in abundance				
Achillea occidentalis	——— ━━━	——— ━━━	———	
Amorpha canescens	——— ━━━	——— ━━━	——— - - - -	
Anemone cylindrica	——— ━━━	——— - - - -		
Antennaria campestris	——— ━━━	——— - - - -	———	
Artemisia gnaphalodes	——— ━━━	——— - - - -		
Asclepias pumila	——— ━━━	——— ━━━	———	———
Asclepias tuberosa	——— ━━━	——— - - - -		
Astragalus crassicarpus	——— ━━━	——— - - - -	——— - - - -	——— - - - -
Baptisia leucophaea	——— ━━━	——— - - - -		
Ceanothus pubescens[4]	——— ━━━	——— - - - -		
Comandra umbellata	——— ━━━	——— - - - -		
Drymocallis agrimonioides	——— ━━━	——— - - - -		
Echinacea pallida	——— ━━━	——— - - - -		
Fragaria virginiana	——— ━━━	—— - - -		
Glycyrrhiza lepidota	——— ━━━	——— - - - -		
Helianthus rigidus	——— ━━━	——— - - - -		
Hieracium longipilum	——— ━━━	——— - - - -		
Kuhnia glutinosa	——— ━━━	——— - - - -	——— - - - -	———
Lepachys columnifera	——— ━━━	——— - - - -	———	———
Lespedeza capitata	——— ━━━	——— - - - -		
Liatris punctata	——— ━━━	——— - - - -	———	———

TABLE 9 *(Continued).*

Species	Western Iowa	Eastern Kan. and Neb.[1]	Mixed Prairie[2]	Plains Dis-climax[3]
Liatris scariosa	——	- - - -		
Lithospermum linearifolium	——	——	- - - -	
Meibomia canadensis and *M. illinoensis*	——	- - - -		
Meriolix serrulata	——	- - - -		
Mesadenia tuberosa	——	- - - -		
Petalostemon candidus	——	- - - -		
Petalostemon purpureus	——	- - - -		
Psoralea argophylla	——	- - - -		
Psoralea esculenta	——	——		
Psoralea floribunda	——			
Rosa arkansana[4]	——	- - - -		
Salvia pitcheri	——	- - - -		
Sisyrinchium angustifolium and *S. campestre*	——	- - - -		
Solidago rigida	——	- - - -		
Solidago rigidiuscula	——	- - - -		
Vernonia baldwini	——	- - - -		
Viola papilionacea	——	- - - -		
Viola pedatifida	——	- - - -		
Species mostly of mixed prairie and short-grass plains disclimax				
Allionia linearis		——	- - - -	- - - -
Allium nuttallii		—	- - - -	- - - -
Ambrosia psilostachya		- -		
Astragalus missouriensis				
Astragalus mollissimus				
Astragalus shortianus				
Cheirinia aspera				
Cogswellia macrocarpa			——	——
Cogswellia orientalis			——	——
Galpinsia lavandulaefolia			- - - -	- - - -
Gaura coccinea			- - - -	- - - -
Grindelia squarrosa				
Gutierrezia sarothrae			- - - -	- - - -
Hymenopappus corymbosus				
Leucelene ericoides			——	——
Linum compactum			- - - -	- - - -
Lygodesmia juncea		——	- - - -	- - - -
Oxytropis lambertii				
Parosela enneandra				
Pentstemon albidus				
Phellopterus montanus			——	- - - -
Psoralea cuspidata				
Psoralea tenuiflora			- - - -	- - - -
Sideranthus spinulosus			- - - -	- - - -
Solidago mollis		—	- - - -	
Sophora sericea				
Stenosiphon linifolius				
Thelesperma gracile				
Species that increased in abundance				
Acerates spp.	——	+ + + +	- - - -	
Allium mutabile	——	+ + + +		
Anemone caroliniana	——	+ + + +	- - - -	
Aster multiflorus	——	+ + + +	- -	
Cirsium undulatum		+ + + +	- - - -	- - - -
Delphinium virescens	——	+ + + +		
Erigeron ramosus	——	+ + + +		
Malvastrum coccineum		+	+ + + +	+ + + +
Opuntia humifusa[5]		+	+ + + +	+ + + +
Oxalis violacea	——	+ + + +		
Senecio plattensis	——	+ + + +		
Solidago glaberrima	——	+ + + +	- - - -	
Tradescantia bracteata	——	+ + + +		

[1]Eastern one third of Nebraska and eastern half of northern Kansas.
[2]West of Nelson, Nebraska, and Montrose, Kansas, to meridian 100.5°.
[3]Kansas and eastern Colorado west of 100.5° meridian.
[4]Shrub which behaves as a forb under annual mowing.
[5]Also *O. macrorrhiza*. All of the cacti have increased more or less.

FIG. 43. *Anemone caroliniana* has greatly increased its numbers as a result of drought and bared soil. Montrose, Kan., May, 1940.

Cogswellia, and *Leucelene ericoides*. Fourteen species disappeared as drought continued, and the remaining all lost heavily in numbers.

The last group includes the most important species that have increased somewhere throughout the grassland during drought. The remarkable ability of certain plants, formerly of little importance, to invade the areas bared by drought is of much interest. *Anemone caroliniana* has spread thickly over wide areas (Fig. 43). During certain springs the soil was so dry that the plants were only 2 inches high and failed to flower, but when the soil was moist as many as 65 blossoms, often 2 inches in diameter, occurred per square meter. The naked flower stalks were sometimes 8 to 10 inches tall.

Oxalis violacea frequently formed circular patches 20 feet in diameter in which the foliage, 2 to 3 inches tall, completely concealed the soil. Like the windflower, it grew best in mellow, bared soil and also between the mats of blue grama, but practically never in dense stands of wheat grass (Fig. 44).

FIG. 44. Characteristic patch of *Oxalis violacea.* Like the windflower, it has efficient underground organs of food accumulation and escapes drought by early growth in spring. Nelson, Neb., May 10, 1940.

Tradescantia bracteata, a species with fleshy roots, was common in patches of variable size, the largest observed being about two acres. Plants grew thickly and, like the preceding, were at a maximum in 1940.

The bulbs of *Allium mutabile* thickly filled the soil over wide areas, even where a fairly good sod remained (Fig. 45). Westward, dense patches of *A. nuttallii* of great extent made beautiful the landscape in spring and early summer. Acerates, *Aster multiflorus, Cirsium undulatum, Malvastrum coccineum,* and *Solidago glaberrima* all have underground stems where much food is stored. *Erigeron ramosus*

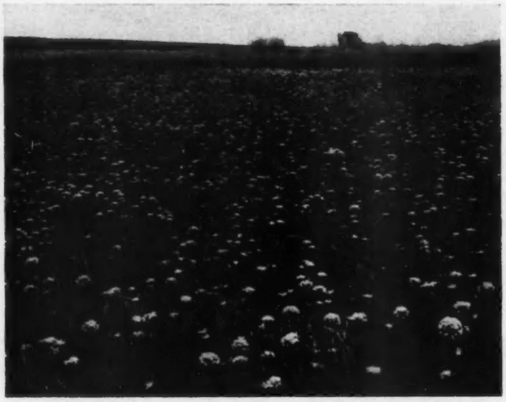

FIG. 45. A dense stand of *Allium mutabile* in bluestem prairie near Jamaica, Neb. Several species of this bulbous forb spread widely during the drought. June 10, 1939.

is a winter annual. The thick-rooted larkspur *(Delphinium virescens)* has increased greatly in abundance, and in places these usually solitary plants were rather closely grouped. All these species have been favored by a marked decrease in competition with other prairie plants. Many evade atmospheric drought by growing only in spring. Others, as Malvastrum, Aster, and Solidago, are very drought-resistant, the aster and goldenrod resuming growth in autumn, if rains come, after the tops have been completely killed by summer drought.

RESURVEY OF UNDERGROUND PLANT PARTS

A resurvey of underground plants parts should be prefaced by a brief statement concerning the soil, the previous depth and distribution of the roots of prairie plants, and the effects of drought in modifying the conditions of the soil.

THE SOIL

From the Prairie soil of Iowa to the Chernozem of the western portion of true prairie, rich, deep, black, fertile, silt-loam soils prevail. The mellow, granular, dark-colored topsoil, enriched by thousands of generations of grasses, extends usually to depths of 12 to 20 inches. Beneath is a zone with higher clay con-

tent and lighter color, which extends to a depth usually of 3 to 4 feet. When dry, this clay-rich soil shrinks considerably and cleaves into vertical columns (technically prisms), often 2 to 4 inches in width and of variable length—4 to 12 or more inches. Vertical cracks and some horizontal ones result. These are usually only a few millimeters in width but in extreme drought are sometimes 2 centimeters wide. Underlying the soil (solum) is the parent material. It is often yellowish or at least lighter in color than the solum, partly because of its lower content of organic matter and partly because it is rich in lime. In Iowa and eastern Nebraska (Prairie soils) there is no lime layer, but in the Chernozem it is found first at 5 to 6 feet in depth but becomes shallower westward where a lime layer often 6 to 18 inches thick occurs. Except for rare rock outcrops, the parent material or massive layer reaches many feet in depth. Although the lime has been eluviated from the A and much of the B horizons, the soil is neutral or only slightly acid, since a constant supply of lime is brought to the surface by the grasses and deposited there when they die (Kellogg 1936). With decreasing precipitation in western Kansas and eastern Colorado the vegetation becomes sparser, the soil becomes lighter in color, and the solum thinner. In these Dark Brown and Brown soils, roots are shallower but very abundant.

Predrought Distribution of Roots in True Prairie

In true prairie roots extend widely and deeply. Those of the grasses commonly penetrate 4 to 7 feet. Only a few are shallower. Forbs are also deeply rooted and the roots commonly spread 2 or more feet laterally on all sides of the base of the plant. A very few species of these prairie plants have underground parts confined to the surface 2 feet; many are 4 to 5 feet deep; but about 65 percent of the forbs have roots that reach depths quite below 5 feet, a penetration of 8 to 12 feet being common and a maximum depth of over 20 feet sometimes being attained (Weaver 1919, 1920). In fact, the semiarid atmospheric conditions promote high water loss, and extensive root development occurs in the deeply moist but well-aerated soil. It is in eastern Nebraska and Kansas that root penetration is greater than anywhere farther westward or eastward in North American grasslands. Westward it is less because of dry subsoil (Albertson 1937; Weaver 1915, 1917). With increasing soil moisture and less evaporation eastward, as in Illinois, the same species root more shallowly (Sperry 1935).

Water Infiltration

Root penetration during drought has been directly correlated with depth of moist soil. The grasses and forbs died in 1934-1936 only after they had exhausted the available water in the surface few feet of soil. The light showers of drought years or even scattered heavy rains were inadequate to moisten again the third, fourth, and fifth foot or at least all parts of this dry layer. Consequently, plants with roots not already established in the deep, moist subsoil were barred from entering it (in many areas) by 2 or more feet of permanently dry soil. Dependence upon current precipitation became much greater. But with the profound disturbance of the plant cover and its disappearance in places, the rate of entry of water into the soil was greatly decreased. This decrease in rate of infiltration profoundly affected root distribution.

Before presenting experimental evidence, the general statements may be made that bared soil greatly retarded water infiltration, that any type of cover living or dead promoted it, and that soil under the native prairie grasses absorbed water much more rapidly than soil covered with the great invader, western wheat grass.

Preliminary experiments were made in a prairie at Lincoln where the bunches of grass were about 12 inches apart but where the low-growing, interstitial species, including bluegrass, had been killed by drought. The soil was a very fine sandy loam, lightly covered with debris, and at the time of the experiments in midsummer it was dry. Water was sprinkled upon the dry vegetation and soil uniformly over an area of about 2.5 by 8 feet for a period of 30 minutes. The amount used was approximately equivalent to 1.6 inches of rainfall. Some water was intercepted by the foliage and evaporated without reaching the soil. A small amount was lost by runoff. Immediately after sprinkling a shallow trench was dug throughout the length of the area of wet soil and depth of water penetration was measured. The transition between the wet black soil and the lighter-colored dry earth was distinct. The soil between the bunches was well occupied by laterally spreading roots of the grasses, at least below a depth of 2 inches.

The dense bunches of little bluestem lessened the depth of infiltration directly beneath them often to only half of the usual 6 inches which occurred between the bunches. There was an exception in one instance where the center of the bunch was dead and decayed. Infiltration under the bunches of prairie dropseed was not as great as between them where the soil was well mulched with dead leaves. But where bare soil occurred between bunches of needle grass, infiltration was much less than that beneath the clumps; otherwise there was little retardation of infiltration by the moderately sized, relatively recently established bunches. Maximum depth of water infiltration anywhere did not exceed 9 inches.

Similar experiments were performed in another prairie where large patches of bare soil alternated with grass-covered land. The dimensions of the watered area were about 6 by 2 feet. Here the granular layer of silt-loam soil was 12 inches deep and very dry. The drought-bared areas had all lost some soil, as is usual, by wind and water erosion, and were in consequence depressed about an inch below the general soil level. When 1.4 inches of water were added in 30 minutes to a dense stand of

blue grama and bare soil, depth of penetration averaged 9 and 2 inches, respectively, and maximum depth in the same order 12.5 and 3.25 inches. Here, as before, depth of infiltration was determined immediately (Fig. 46).

In a second experiment, 2.8 inches of water were sprinkled upon another lot of blue grama and bare soil over a period of 1 hour. Average depth of moist soil immediately after sprinkling was 20.5 inches under the grass but only 11.5 in bare ground. A crack occurred at a few inches depth in the bare soil which permitted water penetration to 22 inches; numerous cracks at 12 inches beneath the sod allowed water to penetrate to 24 inches. Grass roots extended laterally 7 inches into the bare area (Fig. 46).

A third experiment was similar to the first in amount and time of application of water, but the grass was big bluestem. The bare soil without debris was depressed an inch below the general level. Also, as before, a thin sheet of water constantly covered this soil during the sprinkling. The results are shown

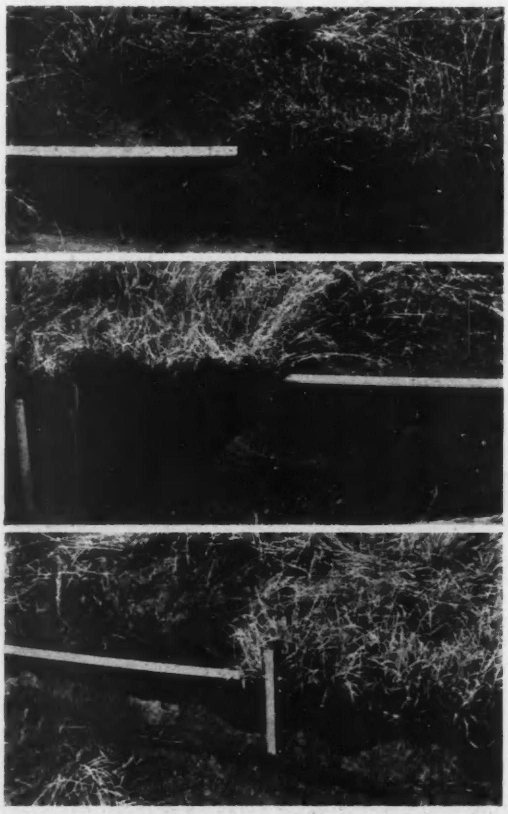

FIG. 46. Depth of water penetration in dry soil: (upper) where 1.4 inches of water were sprinkled on blue grama and bare soil in 30 minutes; (middle) where 2.8 inches were sprinkled on blue grama and bare soil in 60 minutes; and (lower) where 1.4 inches were sprinkled on big bluestem and bare soil in 30 minutes.

in figure 46. Water infiltration under the 2.5-foot length of bare soil occurred to an average depth of 3 inches only. The minimum depth was 1.5 inches and the maximum 3.5. But under the bluestem sod, an average depth of 7 inches was found; minimum infiltration was 6 inches and maximum 9.5.

These experiments are representative of many others which gave similar results, infiltration into bare soil being least and through big bluestem sod greatest. Under western wheat grass, rate of infiltration was intermediate, averaging 5.5 inches compared with 7 inches under blue grama and 9 inches under big bluestem.

The rate of entry of water was measured for bared soil, for soil covered with bluestem or other predrought native grasses, and for the same soil clothed with western wheat grass. In these experiments steel cylinders one square foot in cross-sectional area and 4 inches long were used. The cylindrical wall was only 2 mm. thick, and the steel was sharpened; hence, when it was oiled it could easily be forced vertically into the soil to a depth of 3.75 inches. Water was then added, as rapidly as it could be absorbed, from a sprinkling can with small perforations until an amount equalling 1.6 inches of rainfall had been applied. The time for the infiltration of the water was recorded. Data were obtained from eight widely separated prairies; six were in southeastern Nebraska and two in north-central Kansas. All were on soils of silt-loam texture but variable, of course, in proportions of sand, silt, and clay. The pairs of experimental areas were never more than 9 feet apart and sometimes only 6 feet. The results are shown in table 10.

TABLE 10. Minutes required for the infiltration of an inch of water sprinkled on one square foot of soil which was either bare or clothed with western wheat grass or with other prairie grasses.

Station	Bare soil	Wheat grass	Other grasses	Station	Bare soil	Wheat grass	Other grasses
Lincoln........	33.0	30.0	6.5[1]	Hebron.........	....	9.0	6.0[1]
"	27.5	27.5	6.5[1]	"	....	11.0	8.0[2]
Pleasant Dale...	16.0	13.5	7.5[1]	Nelson..........	17.5	18.0	5.0[3]
" " ...	10.0	6.5	4.0[1]	Montrose........	21.0	12.5	5.0[1]
" " ...	17.0	....	8.5[2]	Belleville........	11.5	11.5	8.5[1]
" " ...	20.0	....	3.0[1]	Clay Center.....	13.5	7.5	3.0[1]
Carleton.......	....	21.0	8.0[1]	" "	11.5	10.5	5.5[4]
"	....	17.0	11.0[1]				
"	19.5	....	9.5[2]	Average, all trials	18.2	15.0	6.6

[1]Big bluestem. [2]Blue grama. [3]Side-oats grama. [4]Pennsylvania sedge.

If the average time for infiltration under the predrought grasses is considered as 1, those under wheat grass and into bare soil are 2.3 and 2.8, respectively.

The rate at which the dry prairie soil absorbed water when populated with an average cover of bluestem grasses and the heavy rainfall required to wet the soil to the depth of little bluestem roots were ascertained by experiment. A prairie at Lincoln on a gentle lower slope on Lancaster silt-loam soil was used. Five-inch boards, five-eighths inch thick, were placed on edge on the sides and ends of a plot 5

feet long and 3 feet wide. This was done by digging a trench four inches deep around the plot and staking the boards tightly against the sides and ends of the block of soil. Soil was then tamped firmly in the trench back of the boards. Water was added from several sprinkling cans simultaneously over the area but only as rapidly as it could be absorbed. In this manner a volume of water equivalent to 11 inches of rain was applied and absorbed in 4 hours. Two days were allowed for the water to reach an equilibrium in the soil after which a deep trench was dug across the lower third of the area and the depth of water penetration mapped as shown in Figure 47.

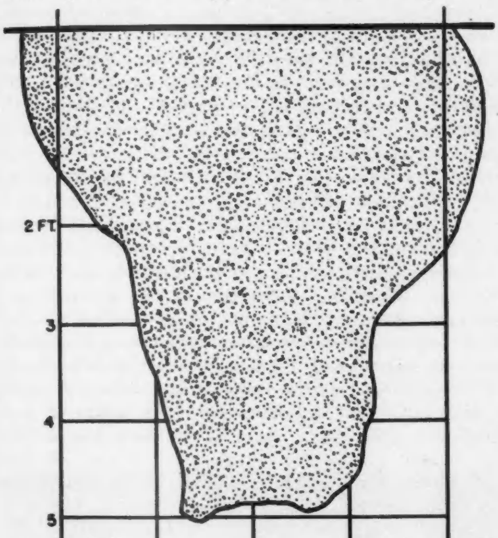

FIG. 47. Diagram showing depth of penetration of 11 inches of rainfall into dry soil covered with bluestem grasses. The water was applied by sprinkling and without runoff in 4 hours and the soil was examined two days later.

The 11 inches of water moistened the soil to field capacity to a depth of about 4 feet. Penetration was fairly uniform and there was no wide lateral spread of water as occurred in similar experiments in cultivated soils at the depth of the furrow-slice.

In a similar experiment in the same area with bluestems and western wheat grass, respectively, the first plot absorbed an equivalent of 7.27 inches of rainfall in 1.5 hours and the soil became wet to a depth of 29 inches. Soil covered with western wheat grass absorbed only 2.98 inches of water which moistened the soil to an average depth of 10.4 inches (Weaver 1942).

A survey of depth of moist soil from eastern Nebraska, through northern Kansas into eastern Colorado was made in June after the wet spring of 1941. It was found repeatedly that moisture penetrated more deeply in the prairies and ranges where a good cover of vegetation remained than it did 2 to 5 feet distant where the soil was bare (Table 11).

TABLE 11. Depth in inches of penetration of rainfall into bare soil and into soil covered with native grasses, mostly short grasses.

Station	Bare soil	Sod	Station	Bare soil	Sod
Lincoln, Neb.	22-23	32-38	Brewster, Kan.	16-20	40-43
Holdrege, Neb.	11-12	18-24	Goodland, Kan.	16-18	18-24
Alma, Neb.	18-22	19-24	Kanarado, Kan.	18-21	27-48

Differences in depth of soil moisture penetration at Lincoln, after a rain of 1.1 inches in August when the soil was very dry, were ascertained by a series of 16 measurements in the prairie. Moisture in bare places averages 3.7 inches deep, that under western wheat grass 4.0 inches, and that under bluestems 6.8 inches. These differences are representative of numerous other measurements made throughout the drought years.

Robertson (1939) worked in these same prairies after 3 years of drought and compared rate of water penetration. He used steel cylinders 4 inches in diameter which were pressed into the soil 14 inches deep. Four inches of water were added to each cylinder, an inch at a time. Big bluestem soil absorbed most readily, soil occupied by wheat grass very much less rapidly, and bared soil least rapidly of all.

The reason for these differences seems clear. On soil without a cover of vegetation or debris, the impact of raindrops or of water sprinkled on the surface loosens the soil particles which are then suspended in the water. This water in entering the soil pores carries the fine, suspended particles with it. The pores are more or less completely clogged on the surface and a compacted layer of soil formed (Lowdermilk 1930). This layer greatly decreases absorption and increases water loss by runoff. Western wheat grass has invaded many areas upon which wind-blown dust has been deposited and through which water infiltrated only slowly. But even where the soil was not dust-covered, this grass has furnished little debris during the drought years and much bare ground is exposed. On soil with a complete cover of true prairie grasses, runoff water is clear (Weaver and Noll 1935). The effects of living and dead roots of different grasses upon the movement of water through the soil, once it has gained entrance, await study. A closely connected problem is their effect upon soil granulation and consequent infiltration rate (Pavlychenko 1941).

Recent studies by Duley (1939) and Duley and Kelly (1939) with mulches on cultivated soil have shown that this clogging of the soil pores and "the development of a condensed layer on the surface of cultivated bare soil has far greater effect on the intake of water than differences in soil type, degree of slope, previous moisture content of the soil, or the rate of rainfall. In fact, . . . it seemed to have a

greater effect than all these other factors combined." Soils covered with a crop had a much higher rate of infiltration of water than bare soils and the more dense crops like native sod and alfalfa had the highest infiltration rates, and these rates were maintained throughout the longest period. Thus, conditions on the soil surface greatly influence water content of soil, and this in turn is a controlling factor in distribution of roots of the grasses and forbs.

Underground Plant Parts in True Prairie

A resurvey of underground plant parts involved examination of prairies of several different types. It included (1) relic grassland where the original plant population was little affected, at least above ground; (2) a study of badly denuded areas where only widely scattered relic or invading grasses occurred; and (3) an examination of half-bared places where relic grasses or invading species occupied the land.

Near the end of the drought, grasses and forbs were examined on both east and west hillsides at Valparaiso, Nebraska, where large local patches of vegetation, each several square rods in area, had escaped with little damage. A large cut, many feet deep, made through the hill in road construction revealed no differences in soil in the places below or above these patches where vegetation had been badly damaged. Nor were differences found in soil characteristics, except in water content, in the deep trenches prepared for root excavation. Under the intact sod, moist soil, except in the surface, was continuous to greater depths than the roots penetrated. *Andropogon furcatus* had normal predrought development throughout a root depth of 7 to 8 feet. *Sporobolus asper* had an abundance of well-branched, strong fibrous roots to 6 feet in depth and some penetrated the moist soil to 7 feet. *Stipa spartea* was even more deeply rooted than previously found (Weaver 1919, 1920). Depths of 5 to 6.5 feet were common and roots of some plants extended downward nearly 8 feet. The prominent taproots of *Psoralea floribunda* were traced to their usual predrought depth of 7 to 9 feet. Three plants of *Liatris punctata* were examined. They showed normal predrought conditions in every respect and no modification was found in the root system that could be attributed to drought. They penetrated to a depth of 9 to 10 feet. A plant of *Kuhnia glutinosa* with 31 stems and a height of 16 inches had a taproot 2 inches thick. It was traced to a depth of 11 feet where it and some of its major branches, which were still 2 mm. in diameter, followed a downward course in the moist soil. This root system was normal as compared with those of similar plants examined several years earlier when rainfall was near the mean.

These results are representative of those obtained elsewhere and illustrate the fact that in many areas of relic vegetation, little or no death resulted underground. This is further confirmed by the lack of an abundance of dead roots, which were commonly found elsewhere, and the persistence of *Andropogon scoparius,* a dominant grass which resisted drought least.

From a typical prairie near Pleasant Dale, Nebraska, representative of numerous others of the more open type, samples of soil for study of root content were taken in midsummer near the end of the drought. They were obtained to a depth of 4 inches only and between the scattered bunches or sods of grass in such a manner that no soil was obtained except at a distance of at least 5 inches from the base of any perennial grass. The samples varied from 9 by 12 inches to 16 by 36 inches in surface area. The interstitial vegetation, if any, consisted of seedling grasses, young plants of *Aster multiflorus,* or an occasional plant of *Salsola pestifer.* The chief grasses were big bluestem, needle grass, tall dropseed, prairie dropseed, and blue grama. Fifteen samples, representing an area of 21 square feet, were thus removed and the living roots separated from the soil, dried and weighed. So sparsely was the soil occupied that the total weight of roots was only 64 grams. This is approximately only 4 percent of the dry weight of the original root mass (Weaver and Harmon 1935).

Trenches dug in this prairie revealed a granular layer of soil only 8 inches deep overlying the pronounced prismatic B horizon which was dry and hard and the prisms much shrunken, exposing great vertical cracks and fissures. Some of the larger cracks extended to the soil surface and thus permitted rapid loss of soil moisture to depths of several feet (Fig. 48). In this dry soil, the widely

FIG. 48. Wall of trench where root systems were examined showing dried and cracked soil to a depth of about 4 feet. Pleasant Dale, Neb., July, 1940.

spaced relic bunches of *Stipa spartea, Andropogon furcatus, Sporobolus asper,* and mats of *Bouteloua gracilis* were examined. Roots were distributed somewhat irregularly on the faces of the prisms, and especially in the deeper crevices where water penetration was not uniform. Roots of needle grass were abundant to 2.3 feet; very few extended deeper. Those of blue grama were abundant to a similar depth, as were those of the other species. Lateral spread of roots was more pronounced in every in-

stance than where these grasses grew in competition with closely adjacent plants. Dead roots were abundant everywhere and especially noticeable in dry soil below the penetration of the living ones. They occupied layers of soil which had not been moistened since the early years of the drought. Repeated soil samplings and root studies elsewhere showed that the conditions of underground plant parts here described recurred again and again over widely separated areas.

Studies in vegetation where relic big bluestem had spread to reclaim drought-damaged territory and occurred in contact with pure stands of western wheat grass were conducted in several prairies. These were made near the end of the drought. The first was on a west slope in the prairie used for experimental purposes near Lincoln. Western wheat grass was 2 feet tall and had headed normally; big bluestem at the opposite end of the trench was 14 inches high. Soil under western wheat grass contained large quantities of dead roots of other grasses, especially bluestems, the chief previous occupants. Roots of the invader followed the old channels of the former bluestems to a remarkable degree. They were often encased for a distance of several inches by the reddish brown cortex of these dead roots. Penetration was only to the dry soil at a depth of 2 feet. Roots were exceptionally well branched and laterals were unusually long. The grass had absorbed the water in the surface 2 feet, where the soil was now (May 31) very dry. Big bluestem had living roots to the depth of moist soil, about 33 inches. At greater depths only dead roots were found. The strong, deep taproots of *Psoralea floribunda* and *Kuhnia glutinosa,* which had survived the drought, extended through several feet of dry soil, in which water content was so low that grasses could not grow, to the deeper soil below 5 feet which had been moist since the beginning of drought.

Another trench was dug on May 30, at right angles to the slope on a north hillside. Formerly the whole hillside was occupied by prairie grasses common to the little bluestem type which included a large percentage of big bluestem. Drought had killed nearly all of the little bluestem, whose place had been taken by big bluestem, *Carex pennsylvanica,* and *Aster multiflorus.* There was a good cover of vegetation. Wind had drifted in dust to a depth of 2 to 4 inches from an adjacent field and smothered the grasses on a part of the slope. This territory was then invaded by western wheat grass in 1936-1938. By 1940 it formed a good stand. No other perennial grasses or forbs occurred where western wheat grass grew.

One end of the 7.5-foot trench was in pure wheat grass; the other end was in prairie undisturbed except by the loss of little bluestem. The transition zone near the middle of the trench, where western wheat grass and bluestem intermingled, was 18 inches wide. The average depth of root penetration under western wheat grass was only 29 inches. The maximum depth was 31 inches, except near the transition zone where the soil was moist to 37 inches. At greater depths the soil was dry and no living roots were found. An abundance of dead roots of the bluestems and other prairie plants including *Equisetum laevigatum, Echinacea pallida,* and *Astragalus crassicarpus* revealed clearly the former presence of a different population. Many of these dead roots extended to 56 inches and some were 68 inches deep. Despite the shallow depth of soil moisture, western wheat grass was in excellent condition. The foliage was 20 inches high and the flower stalks 33 inches tall. The plants had headed in a normal manner. The very dry midsummer of 1940 had greatly retarded the growth of prairie grasses and as a consequence wheat grass had invaded big bluestem, forming the present transition area.

At the opposite end of the trench, big bluestem was 10 inches tall and growing vigorously. In this moist soil, the prairie grasses and many-flowered aster reached depths of 43 to 61 inches, depending upon the depth of soil moisture. Here the soil had not only been moistened much deeper but also an available water content of about 8 percent was still present (Fig. 49).

A deep trench, 16 feet long, was dug on a level hilltop 9 miles west of Lincoln, in an area illustrative of the usual depth of moist soil and roots during the late years of the drought. This was done late in July. The granular soil of the A horizon reached a depth of 1.5 feet, the prismatic structure in the B horizon extended to nearly 4 feet, below which occurred the massive soil of the C horizon. Drought was severe, the granular soil was dry, cracks occurred in the B horizon much as shown in Figure 48, and the C horizon was without water available to growth to a depth of 5.5 feet. At a depth beyond that of greatest root penetration of the grasses, the deep subsoil (parent material) was moist.

Wheat grass, which had dried and lost its green color without heading, had, a few years earlier, invaded half of the area trenched. Except for a few deeply rooted, long-lived forbs, it occurred in a dense pure stand. The few plants of *Kuhnia glutinosa* and *Psoralea floribunda* that remained alive were much dwarfed but unwilted. A nearly pure growth of big bluestem formed a sod just beyond. This grass was still green but partly wilted. With it occurred dwarfed specimens of *Amorpha canescens* and *Liatris punctata.*

Roots of western wheat grass occurred in great abundance but to a depth of only 2 feet. They were branched to very near the tip, as is characteristic of this normally deeply rooted grass (5 to 8 feet) when growing in shallow dry soil. The roots of big bluestem, owing to greater water penetration, thoroughly occupied the soil to a depth of 2.5 feet. Forbs were much deeper. Relationships of roots to tops and to moist soil are shown in Figure 50.

Despite the great depth of rooting of most forbs, season after season with intensive atmospheric drought and severe competition for water (especially with wheat grass) in the surface soil had resulted in their wilting and dwarfing and finally in the death

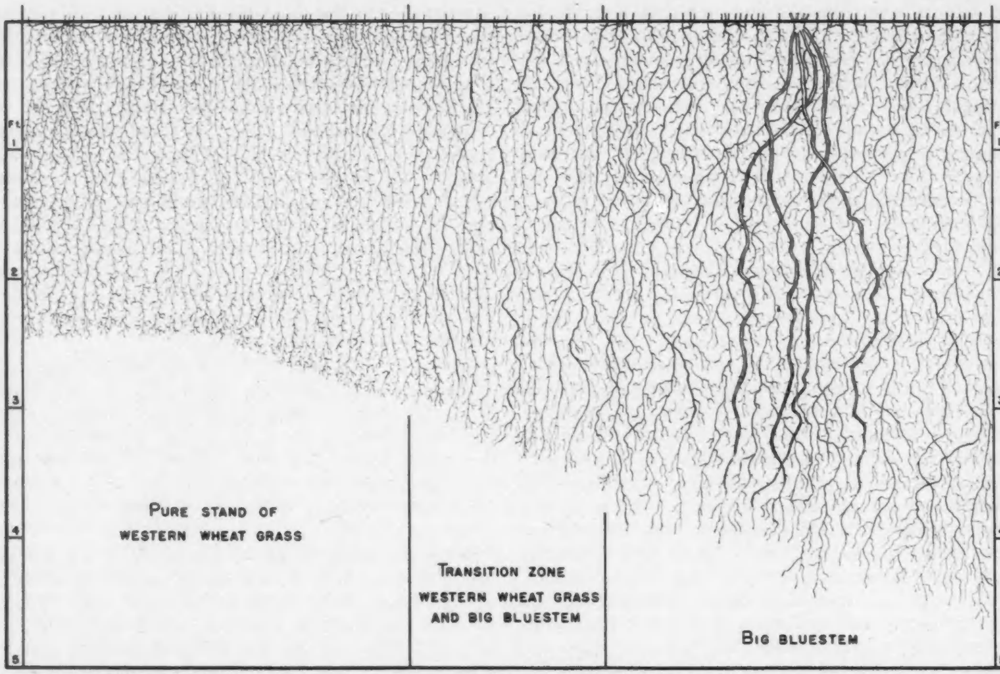

FIG. 49. Diagram showing root depth of western wheat grass above a layer of dry soil, and deeper penetration of roots of big bluestem and many-flowered aster where water penetration was greater and the soil was moist.

of very large numbers. That roots of little bluestem, big bluestem, and other grasses were formerly abundant to 4 to 7 feet was shown by their dead remains, still only partially decayed, in the deeper soil.

It is an important fact that native pastures which were only moderately grazed withstood the drought better than ungrazed prairie (Weaver and Albertson 1936). This resulted from the great decrease in amounts of water absorbed and transpired during the period of intensive atmospheric as well as edaphic drought. Conversely, pastures long overgrazed and hence in the bluegrass stage quickly yielded to drought. Here as in other depleted grasslands, a moist subsoil at 3.5 or 4 feet was common, despite dry soil at this depth in adjacent native prairie. This deeper water was not absorbed because of the relatively shallower roots of bluegrass or weakened little bluestem and other species found in low-grade pastures. The invasion of western wheat grass into the drought-stricken pastures and its early use of available water have greatly retarded the growth of better forage grasses. Sand dropseed, which invaded thousands of denuded pastures over a very wide area immediately following the drought (Weaver and Hansen 1939), has likewise delayed the normal succession by its annual absorption of most of the available water (Weaver and Hansen 1941a).

Rain in the spring of 1941 moistened the soil more deeply and enabled western wheat grass to penetrate to 3.5 to 4 feet in the area shown in Figure 50. Big bluestem extended downward even farther into the newly moistened soil which in July, 1941, was separated from the moist soil below by a layer of dry soil only 6 to 12 inches thick. This occurred despite the comparatively dry midsummer. At this writing (May, 1942) soil moisture in the upper layer is now in contact with that in the deep subsoil and the roots of both seedling grasses and young forbs are growing deeply in the cool moist soil. This condition is quite general. With return of normal rainfall and the consequent increase in seed production, seedling establishment, and vigorous vegetative development, an excellent stand of prairie grasses and forbs will again cover and protect the soil.

UNDERGROUND PLANT PARTS IN MIXED PRAIRIE

Distribution and interrelations of root systems in the short-grass disclimax and the big bluestem consocies were studied and described in 1930-1932 (Albertson 1937). Extensive studies in the short-grass faciation in Colorado had been made even earlier (Shantz 1911; Weaver 1919, 1920). Numerous observations during the drought indicated that both root depth and distribution as well as amount of underground plant parts had been greatly modified. These changes were variable, depending upon the depth of water penetration, number and length of periods without available water in the soil, and often upon the extent to which the grassland had been subjected to grazing. On ranges where deferred grazing was practiced and where the location was such that little dust blew in from adjacent fields, a fairly

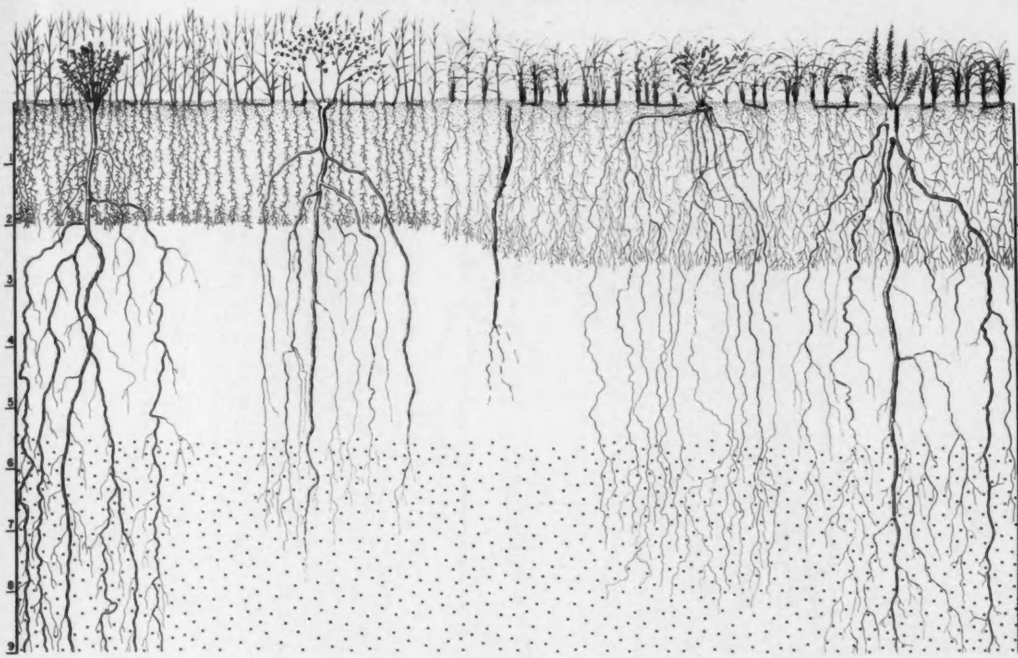

FIG. 50. Relation of roots of ***Agropyron smithii*** (left half of trench wall) and ***Andropogon furcatus*** (right half) and of forbs to moist and dry soil in deep silt-loam soil near the end of the drought. The dry layer between 2-2.5 and 5.5 feet is the result of complete exhaustion of available water by the original plant cover before its death in 1934-1936. The grass roots penetrated only to the depth of currently moist soil. The relic forbs—***Kuhnia glutinosa*** (left) and ***Liatris punctata*** (right)—have survived because their roots are in moderately moist soil between 5.5 and about 16 feet depth. ***Psoralea floribunda*** (left center) and ***Amorpha canescens*** (right center) have also persisted because of deep soil moisture. ***Echinacea pallida*** (center) succumbed to desiccation.

continuous cover was sometimes maintained. But as drought progressed and grazing of the weakened plants was permitted and movement of dust became greater, large areas of range land were rendered completely devoid of vegetation. The dead roots decayed, there was no new growth, and the soil became intensely susceptible to erosion by wind and water.

STUDIES IN THE SHORT-GRASS TYPE

Preceding the dry years, the two dominant short grasses, blue grama and buffalo grass, occupied the soil with a dense mass of roots to about 4 feet in depth, large numbers of the much-branched threadlike roots extending to 5 feet (Fig. 51). The sod was extremely dense, tough, and resistant to erosion. When cut a few inches deep into strips 12 to 18 inches wide, it could be rolled in the manner of bluegrass sod and, like it, used in renewing or establishing a cover of grass elsewhere.

Among the forbs scattered throughout, the roots of *Psoralea tenuiflora, Malvastrum coccineum,* and *Kuhnia glutinosa* penetrated 9 to 12 feet in depth. Consequently, they obtained much of their water supply from the subsoil beyond the extent of the roots of the short grasses. Roots of many other common species of forbs did not penetrate beyond a depth of 5 feet and thus absorbed from the same soil levels as the grasses. The following are representative: *Ambrosia psilostachya, Lygodesmia juncea, Sideranthus spinulosus,* and *Allionia linearis.*

CHANGES DURING DROUGHT

With continued drought, marked changes in rooting habits occurred. The roots of the two dominant short grasses were profoundly reduced in numbers and in depth of penetration. Below 2 feet, roots of these grasses were extremely scarce (Fig. 52). Investigations in widely scattered places on the depth of the penetration of roots on the hard lands in western Kansas and eastern Colorado showed that most of the roots of the two dominant grasses were limited to the upper foot of soil. Here precipitation was less than that at Hays. In many places the cover was so reduced that only small isolated tufts 1 to 2 inches in diameter remained. Spread of the surface roots was usually not more than 6 inches, and although occasionally a root penetrated to 18 inches, nearly all were in the surface foot.

Most of the fully grown forbs established before the drought had succumbed, and nearly all remaining in 1940 were either young plants when the drought began or plants that had become established during the most favorable periods during the drought. For example, the roots of *Psoralea tenuiflora* were nearly

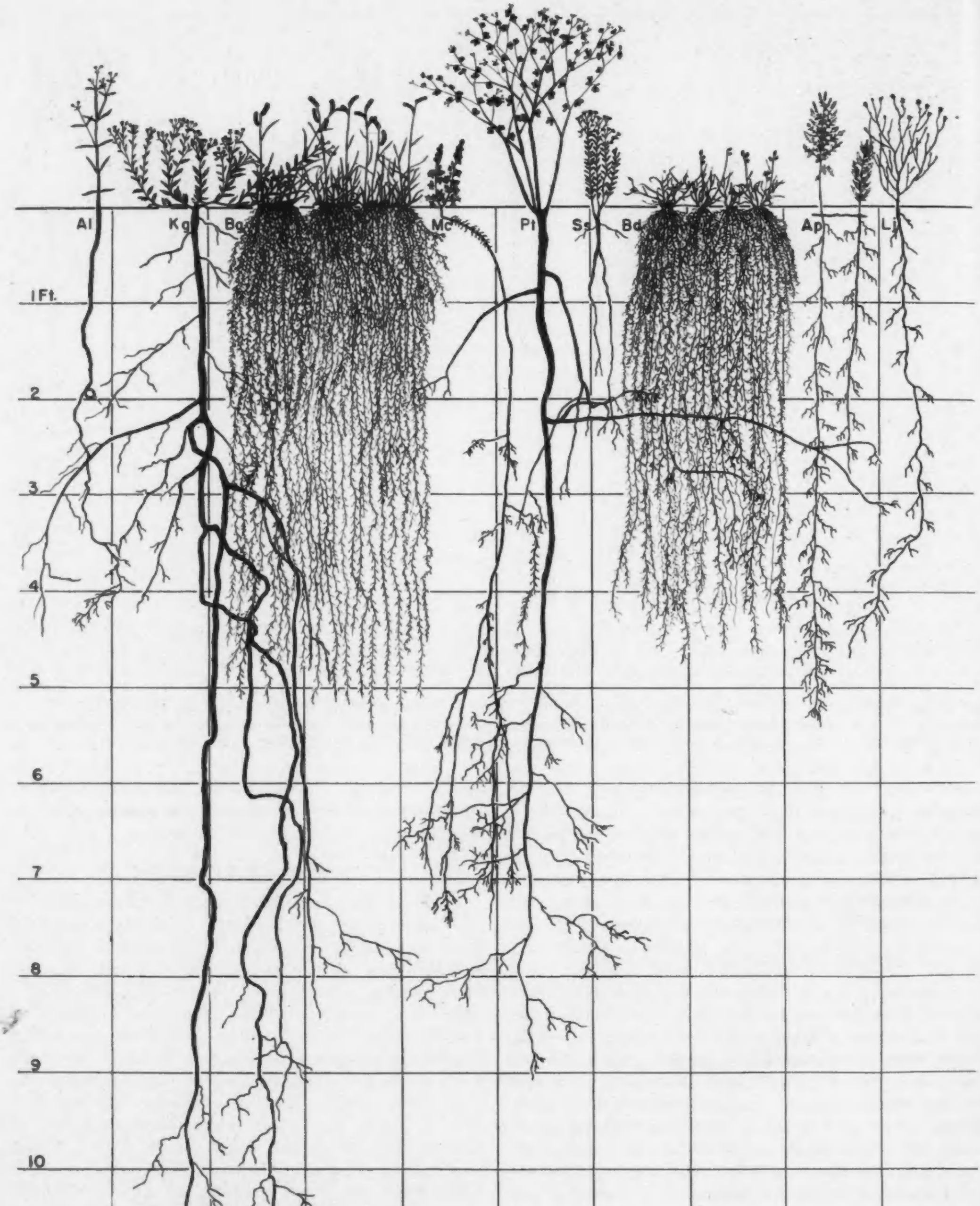

FIG. 51. Root development of native prairie plants in the short-grass type of the mixed prairie at Hays, Kan., before the great drought. Al, *Allionia linearis;* Kg, *Kuhnia glutinosa;* Bg, *Bouteloua gracilis;* Mc, *Malvastrum coccineum;* Pt, *Psoralea tenuiflora;* Ss, *Sideranthus spinulosus;* Bd, *Buchloe dactyloides;* Ap, *Ambrosia psilostachya;* and Lj, *Lygodesmia juncea.*

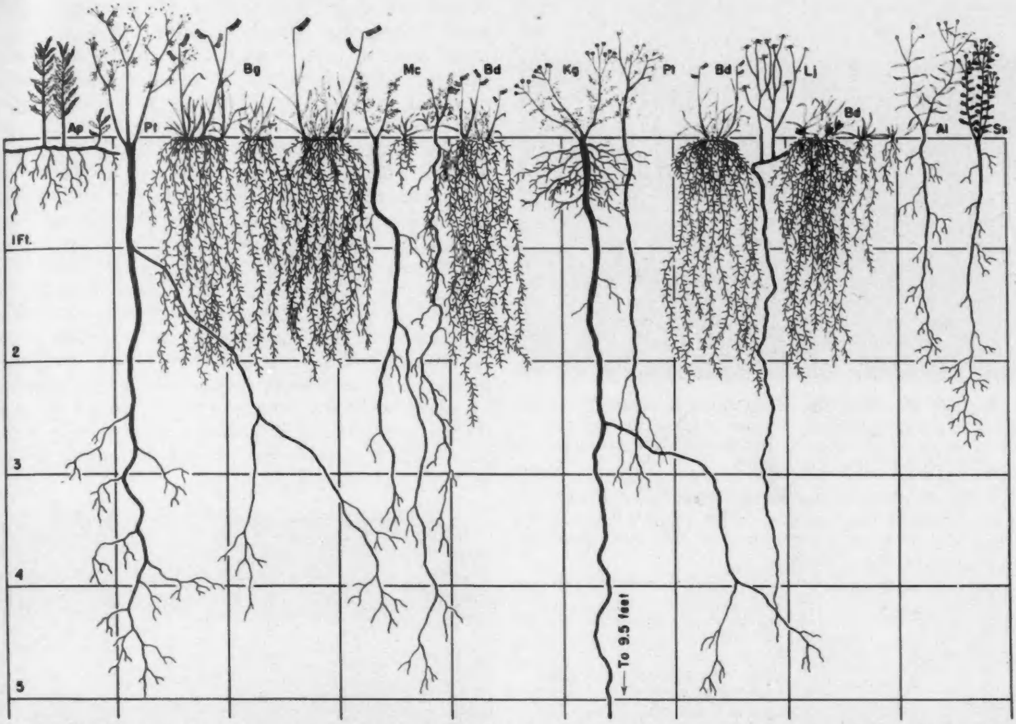

FIG. 52. Root development of native prairie plants in the short-grass type of the mixed prairie at Hays, Kan., at the end of the great drought. Ap, *Ambrosia psilostachya;* Pt, *Psoralea tenuiflora;* Bg, *Bouteloua gracilis;* Mc, *Malvastrum coccineum;* Bd, *Buchloe dactyloides;* Kg, *Kuhnia glutinosa;* Lj, *Lygodesmia juncea;* Al, *Allionia linearis;* and Ss, *Sideranthus spinulosus.*

always much smaller in diameter than those excavated in 1932, and seldom penetrated beyond 4 feet, as compared with a previous depth of penetration of 7 to 9 feet. *Malvastrum coccineum* was one of the few species which increased in numbers, but did so with a greatly reduced root system (Figs. 51 and 52). Only occasionally was a root found to extend deeper than 4 feet. Plants of *Kuhnia glutinosa* in 1932 had roots to a depth of 12 feet in the short-grass sod. But after the drought they were mostly only about half this depth and none extended deeper than 9.5 feet. Little change in rooting habit occurred in forbs whose root systems were formerly limited to 4 feet of soil, although most of them suffered very heavy losses. During the years 1934 to 1939, inclusive, there was a dry layer of soil between 2 and 5 feet in depth underlying the short grasses, at least at the numerous stations where regular soil sampling was carried on. Below this there were small amounts of residual soil moisture available throughout the drought years. The species most successful in surviving the drought were either those with roots that had previously grown into this lower subsoil or those that evaded drought by limiting their activities to short periods (usually early spring) when conditions of growth were most favorable.

QUANTITY OF UNDERGROUND PLANT PARTS

The amount of living underground plant parts in the first 4 inches of soil under the short grasses was ascertained at Hays. Methods used were those described by Weaver and Harmon (1935) and Kramer and Weaver (1936). Samples were taken from adjacent areas where the environmental conditions were approximately similar. In one location the grasses had been protected from grazing since 1932, and had been only moderately grazed previously. The second sampling area had been moderately grazed for 40 years. The third one had been subjected to overgrazing until 1935 when it was further damaged by a covering of dust, and grazing was discontinued. A general view of the conditions of a badly overgrazed range is shown in Figure 53. Samples were taken from carefully selected places to represent average cover in each range—ungrazed, moderately grazed, and heavily grazed, respectively. Basal cover of the three samples was 46, 37, and 21 percent, respectively. These percentages are somewhat higher than the average cover of most western ranges in 1940. The percentage of total cover composed of blue grama grass and buffalo grass, together with volume and weight of the underground parts, is shown in Table 12.

The appearance of the sod before the tops of the

FIG. 53. General view of scattered bunches of buffalo grass and blue grama in western Kansas at the close of the drought. Light-colored bunches are the grasses; the large weeds are Russian thistles.

TABLE 12. Volume and air-dry weight of underground plant parts in the upper 4 inches of one-half square meter of short-grass sod subjected to different intensities of grazing at Hays, Kansas.

Condition	Percent basal cover	Composition of cover in percent		Underground plant parts	
		Blue grama	Buffalo grass	Volume in cc.	Dry weight in gm.
Ungrazed	45.8	26.0	74.0	1,232	276
Moderately grazed	36.6	43.0	57.0	1,114	244
Overgrazed	21.1	55.0	45.0	582	121

grasses were removed, and the underground parts alone are shown for the ungrazed and overgrazed pastures in Figures 54 and 55. Table 12 shows a considerable decrease in both volume and weight from the ungrazed to the moderately grazed pasture. The decrease in volume (53 percent) and weight (56 percent) as a result of overgrazing is very great.

Number of roots per unit area, that extended to a

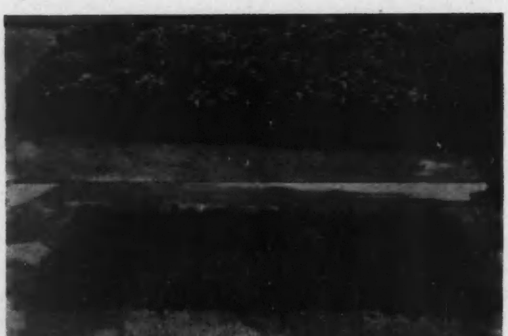

FIG. 54. (Above) Sod of short grass a meter long, one-half meter wide, and one decimeter deep, from an ungrazed range at Hays, Kan. (Below) Underground materials remaining when the soil was removed.

depth of 4 inches, was counted for the three conditions of grazing. Representative one-half square meter samples were excavated to 4 inches depth and inverted. Enough soil was then removed by a gentle spray of water so that the roots protruded. Circles 3.5 inches in diameter were marked off on the sod and all of the roots within these sample areas were counted. They were very uniformly distributed in the protected sod and averaged 45 per circle. But in the overgrazed sod, portions of soil without roots protruding and comparable to the bare patches on the upper surface were common (Fig. 56). The average number of roots in this sample was only 10 per unit area. The overgrazed sod was easily broken and not well held together by underground parts. As shown by Kramer and Weaver (1936), resistance to erosion is, in general, proportional to the quantity of plant materials both above and below ground. Overgrazing and drought often result not only in the loss of the cover of grass but also of the top soil as well.

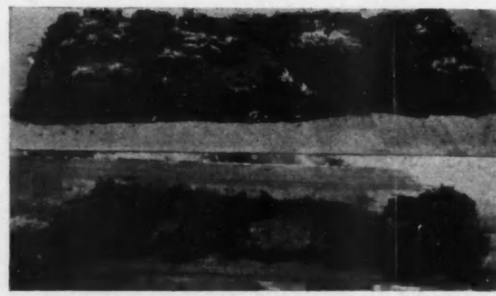

FIG. 55. (Above) Sod of short grass as in Fig. 54, but from an overgrazed range. (Below) Underground materials remaining after the soil had been washed away.

STUDIES IN THE BIG BLUESTEM TYPE

Roots of grasses and forbs commonly found in the postclimax big bluestem before 1933 have been described (Albertson 1937). Bisects were again made in 1940 to ascertain root depth and spread at the end of the drought (Fig. 57). During increase in desiccation the root systems of most species grew into deeper soil and a greater number of rootlets developed at the deeper level. The average root depths in feet of 8 important species before (1932) and near the close of the drought (1939) were as follows:

Andropogon furcatus	5	6
Agropyron smithii	6-7	7-8
Bouteloua curtipendula	5	6
Psoralea tenuiflora	7-8	10
Kuhnia glutinosa	10	12
Aster multiflorus	3	7
Vernonia baldwini	4	8
Salvia pitcheri	4	8

Thus, the roots of all of these species (and others) not only penetrated deeper into the moist subsoil, following drought in the solum, but the roots of Aster, Vernonia, and Salvia doubled their former

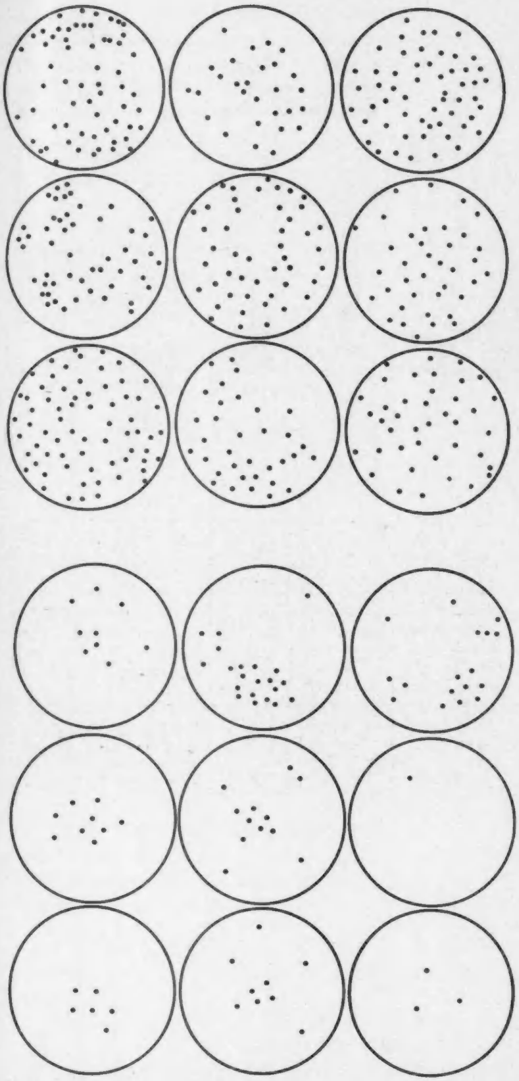

FIG. 56. (Above) Number of roots (dots) of ungrazed short grasses in representative circular areas 3.5 inches in diameter at a depth of 4 inches. (Below) Roots in similar representative areas of overgrazed grasses.

length. The roots of *Panicum virgatum* did not increase beyond their former 7-foot depth, but they became much more numerous than formerly in the deeper soil. Thus, changes resulting from drought in upland and lowland species were quite diverse.

PLANT YIELD IN RELATION TO WATER CONTENT OF SOIL

The yield of grasses and forbs of prairie and the amount of available soil moisture were ascertained during the dry year of 1940 and the moderately wet one of 1941. This survey was a continuation of similar studies in 1939 (Weaver and Albertson 1940). Twelve separate prairies were studied. They ranged from western Iowa to western Kansas and represented four different types of vegetation. Those in western Iowa (Iowa group) were virgin bluestem prairies practically undisturbed by drought. The Lincoln group, including also Hebron, Nebraska, and Belleville, Kansas, were also bluestem prairies but they had been more or less damaged by drought. They maintained a fairly good cover. The third group was characterized by the almost complete loss of bluestems and their replacement by a dense stand of western wheat grass at Carleton, Clay Center, and Montrose (Fig. 1). The most westerly group is in the mixed prairie association but is now clothed only with the most drought-resisting short grasses. Soils are all similar, being of silt-loam texture; although those at Lincoln and eastward belong to the Prairie zonal group, while those under lighter precipitation westward are Chernozems. All are of high fertility, and water is the chief limiting factor to plant growth.

Stations for obtaining samples for water content were selected with reference to typical and relatively uniform composition of vegetation. There were included in each group of stations various gentle slopes and nearly level uplands, where water content of soil depended entirely upon precipitation. Samples were obtained regularly to a depth of 6 feet and at approximately the same time at each of the stations from the middle of April until early in September in 1940, and from May 1 to August 30 in 1941.

Five sample plots, each 4 square meters in area, were staked out in spring in the general vicinity of the soil-sampling areas. They were a few rods apart and selected at random. The vegetation was clipped at a height of 1.5 inches at each subsequent soil sampling, grasses and native forbs (and weeds if present) being harvested separately. These were air-dried and the weight obtained to the nearest gram. From five similar plots in each prairie, total seasonal yield was also obtained at the last clipping. Monthly clippings were made only in 1940, but total seasonal yields were again obtained in 1941 from areas previously undisturbed except by annual mowing.

Basal cover at the several stations was far less than the normal predrought cover, except that of the Iowa prairies where drought had not been severe. The amount of decrease in cover has been determined many times by means of quadrats before, during, and at the end of the drought. At the Nebraska-Kansas bluestem stations it had been reduced to about 33 percent normal. At the stations where bluestems had died and western wheat grass had invaded, the cover was only 20 percent normal. Losses in the mixed prairie resulted in a very open cover, approximately 10 percent of that occurring before the drought.

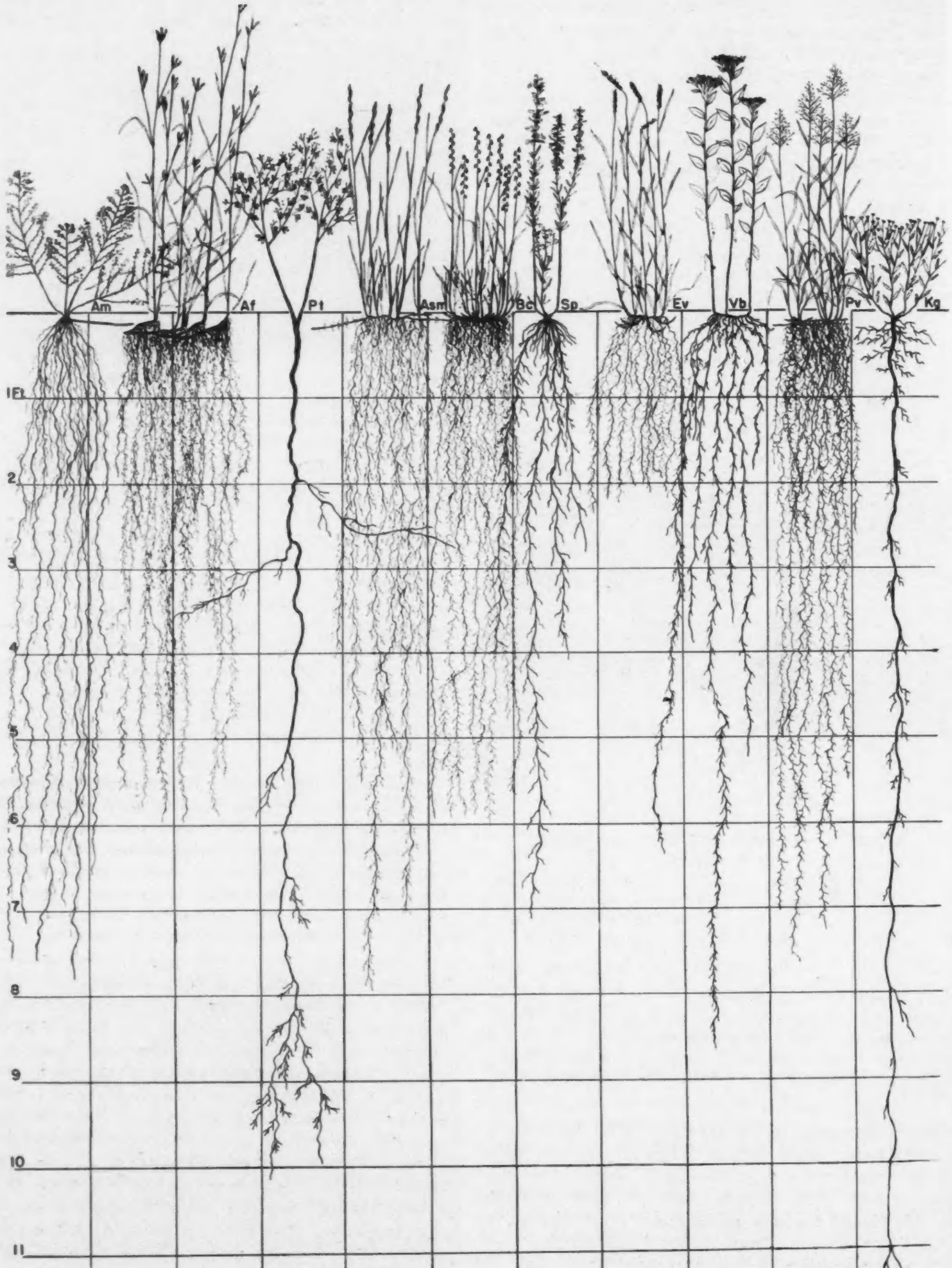

Fig. 57. Root development of native prairie plants in the big bluestem type at Hays, Kan., at the end of the great drought. Am, *Aster multiflorus;* Af, *Andropogon furcatus;* Pt, *Psoralea tenuiflora;* Asm, *Agropyron smithii;* Bc, *Bouteloua curtipendula;* Sp, *Salvia pitcheri;* Ev, *Elymus virginicus;* Vb, *Vernonia baldwini;* Pv, *Panicum virgatum;* and Kg, *Kuhnia glutinosa.*

IOWA STATIONS IN 1940

At the Iowa stations, where the mean annual precipitation ranged from 29.5 to 31.7 inches, rainfall during the several months was not sufficient to keep both soil and subsoil constantly moist (Fig. 58). A constantly moist soil did prevail the previous year (Weaver and Albertson 1940), but the growing season of 1940 was characterized by midsummer drought. This was least severe at the Iowa stations where precipitation was not only highest and best distributed but also because of the ready infiltration of water into the soil which was kept in a porous, water-receptive condition by the continuous cover of bluestem grasses.

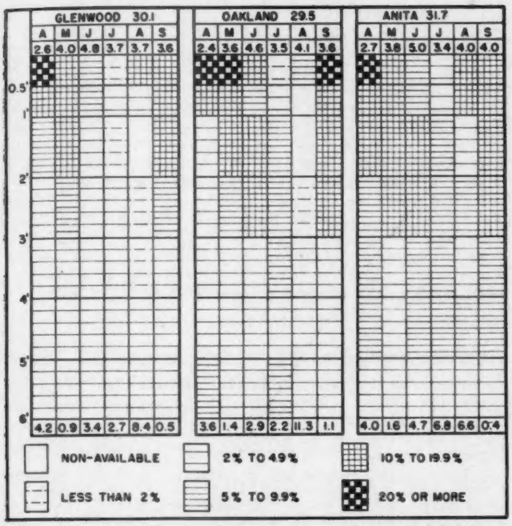

FIG. 58. Available soil moisture to a depth of 6 feet at three Iowa stations during 1940. Mean annual precipitation at each station follows the name, mean monthly precipitation is below the letter indicating the month, and current monthly rainfall is given at the foot of each column.

Monthly rainfall was far above the mean at all stations in April, but below normal for the remaining months except for very heavy rainfall in either July or August or during both months. Soil drought occurred at the first two stations (Fig. 58) in midsummer, and growth was distinctly retarded by temporary unavailability of water in the first or second foot.[4] Available soil moisture in the third foot (and fourth foot at Glenwood) was reduced to less than 2 percent. This greatly affected the yield of vegetation (Table 13).

The low yield of the first clipping at Anita was the result of a late spring prairie fire. Otherwise, yields at this station were consistently high. At the other stations they were somewhat lower in July and decreased greatly in August. The midsummer drought

[4] Total water content of soil minus the hygroscopic coefficient (which was determined for each soil depth at each station) is designated as water available for growth. The hygroscopic coefficient, with few exceptions, ranged between 9.1 and 11.9 percent.

TABLE 13. Monthly and total yield in grams of grasses and forbs at each of the Iowa stations in 1940, and total production of controls.

Date	Glenwood		Oakland		Anita	
	Grasses	Forbs	Grasses	Forbs	Grasses	Forbs
June 6	2,881	502	2,577	444	1,668	230
July 5	1,661	173	1,366	245	1,872	89
Aug. 6	546	63	429	39	1,253	29
Sept. 1	1,200	26	1,088	61	889	10
Total	6,288	764	5,460	789	5,682	358
Controls	6,355	874	5,475	1,118	4,980	679
Total clippings	7,052		6,249		6,040	
Total controls	7,229		6,593		5,659	

was not pronounced at Anita, but at Glenwood the tops of the deeply rooted big bluestem were dry by July 18 and those of little bluestem appeared as if killed by frost. Only the lower one third to one half of this grass remained green. Forbs were affected but little. The grasses were even more greatly injured at Oakland. Here on level upland, both big and little bluestem appeared as if scorched. They had lost their normal color and were two-thirds dry. Forbs alone were green. Renewed growth following the abnormally high August rainfall produced a heavy yield in September. The ability of grasses to revive when rains come is a chief adaptation to semiarid climates. It is of much significance that vegetation in the clipped plots, where decreased transpiring surface had prevented great water losses, remained green and continued growth, despite exhaustion of soil moisture elsewhere.

Total yield of grasses was remarkably uniform at the three stations. There was greater variability in yield of grasses among these stations where a single harvest was made in September. The mature crop in September yielded more grass at two stations than did the total of the four clippings. But it was less at Anita where the late spring burning occurred (cf. Aldous 1934).

Early yields of forbs were high but after a second clipping they decreased greatly (Table 13). Yield of forbs was always greater, of course, where they were unclipped, since clipping is far more injurious to them than to the grasses. The chief forbs were *Amorpha canescens, Euphorbia corollata,* and *Kuhnia glutinosa* although many others occurred. Forbs supplied 14 percent of the total yield of hay in September but only 10 percent when clipped four times. Whether clipped four times or only once per season, the total average yield was practically the same—6,494 grams from the areas sampled or 1.45 tons per acre. This, however, was much greater than in the drier soil westward. Results from clippings at the Iowa prairies are given in Table 13.

LINCOLN STATIONS IN 1940

At the Lincoln stations the mean annual precipitation ranged between 26.2 and 27.9 inches. The

current monthly rainfall at all stations, with few exceptions, was lower and often very much lower than the mean. The only significant increase above the mean was about 2 inches in August at Belleville. Severe midsummer and late summer drought occurred at all stations (Fig. 59).

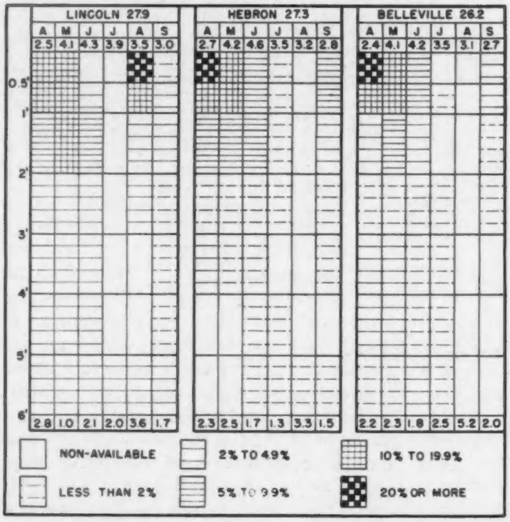

FIG. 59. Available water content of soil, mean annual and mean monthly precipitation, and current monthly precipitation at the Nebraska-Kansas bluestem stations in 1940.

The early growing season was cool and sufficiently moist to promote a good growth of grasses. At Lincoln drought threatened after the middle of May, but although precipitation in June was light, the showers were so distributed that the vegetation made a good growth until late in the month. Then it not only wilted but was greatly damaged by severe drought. The green color of the grasses practically disappeared and the bluestems turned reddish brown as they normally do in October. When trod upon, the grasses crunched like snow. This condition prevailed at all three stations in July. Although the drought at Hebron and Belleville began a little later, it prevailed somewhat longer than at Lincoln, where more than 4.2 inches of rain fell between July 26 and August 4. Here, and after heavy rains at the other stations, growth was renewed (except some plants which had died) and much foliage developed. It was believed that the prairies would be mowed at Hebron and Belleville, hence the controls also were harvested on July 30. At Lincoln they were in a protected area and were left intact until September, when the other controls were harvested for a second time.

Yields of grasses were highest at Lincoln, where a considerable amount of the early growing needle grass was intermixed with the bluestems (Table 14). The July 1 yield exceeded the earlier one at Hebron, where the prairie had been burned, but was considerably reduced at the other stations. On August 1, there was no grass to harvest at Hebron and very little elsewhere. September 1 clippings were the heaviest of the season at all stations, the yield at Hebron being larger than that at Belleville. Total yields of clippings were relatively high despite the midseason drought. They were highest at Lincoln and about the same at the other stations (Table 14). Forbs, with one exception, yielded most at the first clipping. The chief species were *Amorpha canescens, Aster multiflorus,* and *Liatris punctata.*

TABLE 14. Monthly and total yield in grams of grasses and forbs at each of the Nebraska-Kansas bluestem stations in 1940, and total production of controls.

Date	Lincoln		Hebron		Belleville	
	Grasses	Forbs	Grasses	Forbs	Grasses	Forbs
June 1	1,591	230	671	74	1,143	32
July 1	916	40	708	67	635	102
Aug. 1	57	14	0	0	150	7
Sept. 1	2,055	70	1,644	19	1,232	13
Total	4,619	354	3,023	160	3,160	154
Controls July 30	.....	...	1,324	160	1,900	44
Sept. 1	4,303	284	1,288	60	1,371	11
Total	4,303	284	2,612	220	3,271	55
Total clippings	4,973		3,183		3,314	
Total controls	4,587		2,832		3,326	

The total of the four clippings averaged less than the single harvest at Belleville. The average total clipping at the three stations yielded 3,823 grams, the control yields weighed 3,582. The yield of controls was only 0.80 ton per acre and only 55 percent of that at the Iowa stations.

CARLETON STATIONS IN 1940

At the Carleton stations the mean annual precipitation (25.0 to 27.3 inches) was nearly as great as that at two of the Lincoln stations near which they occur (Fig. 60). The great difference lay in the fact that the vegetation had been much more damaged by drought and that relic bluestems had succumbed to the invasion of dense stands of western wheat grass. Precipitation was below normal and nearly always much less than normal, except in April at Montrose and in August at Carleton (Fig. 60). The wheat grass greatly decreased water infiltration and the soil was practically without available water after early summer, except as temporarily moistened by light showers. The grass dried in June without producing spikes. At two of the three stations the wheat grass depended entirely upon the moisture in the surface 2 feet of soil. Water from the deeper soil was apparently removed only by the relic, deeply rooted, xeric forbs which survived the drought because of this deeply rooting habit.

The rolling of the leaves of wheat grass was evidence that water was scarce as early as May 10, and

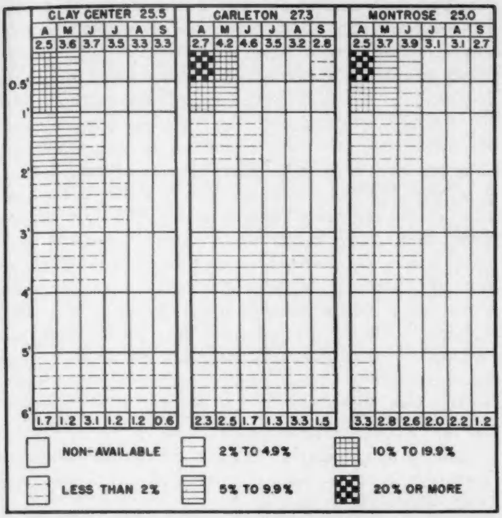

FIG. 60. Mean annual and mean monthly precipitation, current monthly rainfall, and available soil moisture at Nebraska-Kansas wheat grass stations in 1940.

drought became severe by the end of May, when this grass, over one fifth of the prairie at Carleton, was dried and had no green color. Gradually, after a period of wilting and bleaching, the whole prairie appeared tan or yellowish in color and the dried leaves and stems were brittle. The sparse forbs were dwarfed and wilted and many died. The prairie was a sea of dried grasses about 10 inches high and remained thus throughout the summer. There were no seasonal aspects except the prevernal. Only rarely did one of the widely spaced forbs bloom. Conditions were only slightly better at Montrose and somewhat worse at Clay Center, where the vegetation was lightly sprinkled with dust. No late summer development occurred at Clay Center, so meager was the rainfall. But a little growth of wheat grass and side-oats grama occurred at the other stations after the showers in August.

The yield in May was heavy at all stations and especially at Montrose where rainfall was highest, owing to the early awakening of the wheat grass and its rapid development (Table 15). Yield decreased sharply in June. There was none or practically none in July, and only a very light yield, if any, in September. This yield, of course, was made by the utilization of rainfall between the periods of soil sampling (Fig. 60).

Other grasses, mostly side-oats grama and blue grama, were of very minor importance, all yielding heaviest in May and September except at Clay Center. Most of the forbs died, especially following the invasion of wheat grass, and the forb increment of yield was low. This was true also of the weeds which grew at Clay Center.

Total yields of wheat grass varied widely, from 1,645 to 3,507 grams. They were least at Carleton

TABLE 15. Monthly and total yield in grams of grasses and forbs at each of the western wheat grass stations, and total production of controls in 1940.

Date	Clay Center				Carleton			Montrose		
	Wheat grass	Other grasses	Forbs	Weeds	Wheat grass	Other grasses	Forbs	Wheat grass	Other grasses	Forbs
May 31......	1,758	19	68	27	1,436	30	16	3,385	60	12
June 30......	244	26	51	15	185	8	3	25	2	1
July 31......	0	0	16	4	0	0	5	12	2	0
Sept. 3......	0	0	0	0	24	110	7	85	143	2
Total.........	2,002	45	135	46	1,645	148	31	3,507	207	15
Controls......	2,740	23	25	11	1,645	182	179	2,625	16	91
Total clippings.....	2,228				1,824			3,729		
Total yields of controls....	2,799				2,006			2,732		

where the grass absorbed almost entirely from the surface foot of soil and greatest at Montrose where rainfall and soil moisture were likewise greatest. Other grasses also yielded highest at Montrose.

Total yields of clippings were in the same sequence as yields of the dominant grass. Yield of wheat grass from the control plots clipped but once was the same as the sum of the several clippings at Carleton, 738 grams greater at Clay Center, but 882 grams less at Montrose. Total yields of the controls were more uniform for the several stations than were the sums of the several clippings. They were higher, however, but in the same sequence as before, except at Montrose.

Average total clippings at the several stations yielded 2,594 grams; weight of the controls was 2,512 grams. Yield of controls was only 0.56 ton per acre and only 39 percent of that at the Iowa stations, but 70 percent of the yield from the Lincoln bluestem group.

WESTERN KANSAS STATIONS IN 1940

At the western Kansas stations, mean annual precipitation varied from 18.9 to 23.3 inches, thus being about 2 to 8 inches lower than that at the Carleton group of prairies. The current monthly precipitation was far below normal at all stations, except in July and August at Hays, being normal at Phillipsburg in August, and much above the mean at Dighton in May and August (Fig. 61). The mixed prairie had been almost completely reduced, either by drought alone (Phillipsburg) or by long continued grazing and drought (Hays and Dighton), to a short-grass plains disclimax. On each prairie enough silt had been deposited as dust to seal the soil so effectively that runoff was greatly increased. It was further accelerated by the sparse cover of grasses and consequent lack of much obstruction to running water. For example, a 4-inch rain at Hays in July moistened the soil to only 10 to 15 inches. More usually in this arid climate a high monthly rainfall results from

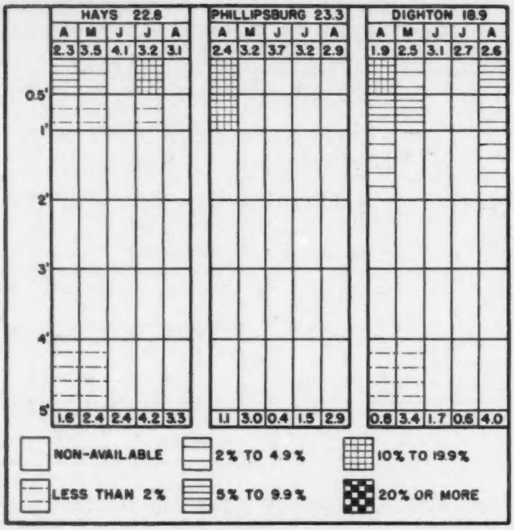

FIG. 61. Chart showing the light current monthly rainfall and small amounts of water available for growth of vegetation at the stations in western Kansas in 1940.

many small showers followed by bright sunshine and high winds; hence the water is soon lost from the soil by evaporation and relief from drought is slight and temporary.

It should be emphasized that blue grama and buffalo grass have the ability to renew growth during the warm season at any time showers provide available water and to become dormant again within a short period of time. Various weeds also start growth promptly and develop vigorously during these intermittent periods with moist surface soil, which monthly soil sampling may not reveal. In fact, weekly sampling at Hays in 1940 and 1941 showed this was the condition.

Not only was the vegetation clipped closer to the soil at these stations, about 0.5 inch, but the clippings were made at irregular intervals. The object was to harvest at such times as to obtain the total yield without the loss of any vegetation. For example, only the weeds were clipped in the plots at Hays and Dighton early in June in order to obtain the crop of *Lepidium densiflorum, Monolepis nuttalliana, Lappula* spp., and *Hordeum pusillum,* which had completed growth, produced seed, and were drying. For the same reason single autumnal clippings of controls were not made.

Drought began early in May at all of the prairies. Although rainfall varied considerably at the different stations, conditions on the prairie at Phillipsburg, which gave an intermediate yield of both grasses and weeds, will illustrate the intensity of the drought. By June 20 conditions were almost tragic. The bluish-gray color of the scattered blue grama indicated severe drought. Little growth had been attained by the sparse native grasses and forbs, although weeds were so plentiful that the yield even from these stunted plants was high. The rolled and twisted leaves of the short grasses did not exceed 3 inches in length. Of the mid-grasses, side-oats grama had not renewed growth, and the wilted shoots of sand dropseed were few. The abundant weeds—species of Lappula and Lepidium, *Hordeum pusillum, Sophia multifida, Plantago purshii,* and *Salsola pestifer*—were extremely small and wilted. The few native forbs were much dwarfed; *Opuntia humifusa* was wilted and had put forth no new branches. Even by July 31, there had been a very meager growth. Only a few short, wilted shoots were found in any tuft of grass. Weeds had produced less forage than the grasses. The profound drought was scarcely relieved by showers until August. By mid-September, growth was complete for the season, since all new vegetation was dry and half dead.

Yield of clippings in Table 16 shows the response measured in dry weight production. Except for weeds, it was very meager.

TABLE 16. Monthly and total yield in grams of grasses, forbs, and weeds at the short-grass prairie stations in west-central Kansas and total production in 1940.

Date	Hays			Date	Phillipsburg				Date	Dighton	
	Short grass	Forbs	Weeds		Short grass	Mid-grass	Forbs	Weeds		Short grass	Weeds
June 10	...	...	982	June 20	124	8	114	1,707	June 11	...	3,210
June 21	346	9	...	July 31	193	13	...	195	June 25	25	.....
July 29	420	2	3	Sept. 17	55	11	25	63	Aug. 1	33	.....
Oct. 2	452	...	...						Sept. 28	184	.....
Total.....	1,218	11	985		372	32	139	1,965		242	3,210
Total clippings .	2,214				2,508					3,452	

The greatest yield of short grasses was at Hays, where the October harvest of grasses was highest, a result of the late summer rains. Three fourths of the yield at Dighton also resulted from rains in August and September. But at Phillipsburg both precipitation and yield in late summer were less. A few relic mid-grasses, mostly side-oats grama, occurred at Phillipsburg. Native forbs were important only at Phillipsburg; none occurred at Dighton. Dighton, however, ranked first in production of weeds and total yield of clippings as a consequence. Phillipsburg was intermediate in both respects, and Hays, although it had the most grass, gave the lowest total yields.

Average yield, 2,725 grams per sampling area or 0.61 ton per acre, is higher than that at the Carleton stations. But when yields of grasses alone are compared, the short-grass stations produced only 26 percent as much as the wheat grass stations and only 11 percent as much as the Iowa stations.

Comparison of Yields

Yields of the several clippings of grasses and forbs, including weeds, and yields of the controls at each station group are shown in Table 17. Figure 70

TABLE 17. Summary table of plant production in grams (in round numbers) at the several stations in 1940.

Yield	Iowa Stations		Western Bluestem Stations		Wheat Grass Stations		Midwestern Kansas Stations	
	Grasses	Forbs	Grasses	Forbs	Grasses	Forbs & weeds	Grasses	Forbs & weeds
Clippings	5,810	637	3,601	223	2,518	76	621	2,104
Controls	5,603	890	3,395	186	2,410	102	...	.....
Total Clippings	6,447		3,823		2,594		2,725	
Total Controls	6,494		3,582		2,512		......	

shows graphically the yield of grasses and native forbs and total yields from the control quadrats where growth was not interrupted by clipping. Examination of these data shows that in 1940 production of grasses decreased directly and greatly from east to west, with corresponding increase in severity of drought. Decrease in yield of native forbs was similar to that of the grasses until the overwhelming crops of weeds were included at the mixed prairie stations. In fact, the weed factor was so great as to upset the very pronounced differences in yield of grass, so that total production in mixed prairie was also higher than at the wheat grass stations.

Relative Height Growth at Times of Clipping

The recovery of plants from clipping and the height attained at the time of the next clipping are of considerable significance. They are not closely connected with soil moisture as shown in the charts for unclipped prairie, since the repeated removal of the tops in itself greatly reduced water absorption and thus conserved the water supply. The removal of the cover even to a height of 1.5 inches, as in grazing, promoted loss of water directly from the soil surface, especially where there was a dearth of litter (R. J. Weaver, 1941). The results are of interest both in regard to rate of regeneration and in reproducing a stand of forage under conditions simulating grazing (Weaver and Hougen 1939).

Height growth of bluestems was progressively slightly less at the Iowa stations with the progress of the season (Table 18). At the second group of bluestem stations, height growth was more uniform but only about two thirds as great early in the summer. It was increased by rains late in summer. An average difference of 6 inches in height of foliage of unclipped big bluestem at the two groups of stations correlates with decrease in water content of soil westward.

The low stature of wheat grass, 10 to 12 inches as compared with a normal height of 30 to 36 inches,

TABLE 18. Average heights in inches of grasses and a representative forb at the several stations at each clipping, and average heights of control vegetation when clipped in September.

Station groups	Species	June	July	Aug.	Sept.	Controls
Iowa	Bluestems	11	9	7	7	16
Lincoln	Bluestems	6	6	6	8	10
Carleton	Wheat grass	12	4.5	..	5	10
Iowa	*Amorpha canescens*	9	6	6	3	19
Lincoln	*Amorpha canescens*	4	5	4	3	7
Carleton	*Amorpha canescens*	3	3	3	2	5

reflects extreme drought. Recovery after clipping was slight and the measurements in July and September represent only a few plants. Times of cutting of short grasses at the western stations were too irregular for comparisons of height growth.

Amorpha canescens was selected to represent the forbs because it was the only species found in most prairies in each of the station groups, because it often occurred in great abundance, and because of its ability to recover regularly after clipping. Nearly all forbs renewed growth to some degree in the moist Iowa prairies, but recovery was less uniform in the Lincoln group, and in the dry soils at the wheat grass stations many forbs did not grow after the first clipping.

Soil Moisture and Plant Growth in 1941

The growing season of 1941 was characterized by a late, wet spring and abundant rainfall in May, June, and July or at least during one or two of these months. The greatest increase in rainfall occurred at the stations in Kansas, where the normal monthly precipitation in June of 3 to 4 inches increased at some stations to 10 or 11 inches. At the short-grass stations, total rainfall for April or May or June was at least twice normal. Vegetation flourished until late summer when moderate drought occurred.

Water content of soil was high to a depth 5 or 6 feet at both Glenwood and Oakland until early in August (Fig. 62). Soil moisture and yields at Anita are not given because of accidental spring burning which depressed growth. The very heavy rains in June added moisture to the deep subsoil and greatly ameliorated conditions of growth when water content was depleted in August, especially at Glenwood. Hence development was not much retarded. The foliage of little and big bluestem attained an average height of 16 and 24 inches, respectively (Fig. 63).

At the Lincoln group of stations both rainfall and soil moisture were less than in Iowa, but the general pattern of water distribution was the same (Fig. 64). Conditions of growth were poorest at Lincoln, since the 11 inches of rainfall in June at Hebron and Belleville did not occur there. But they were more favorable than during 1940, despite the severe drought during July and August, which caused the vegetation to wilt and dry.

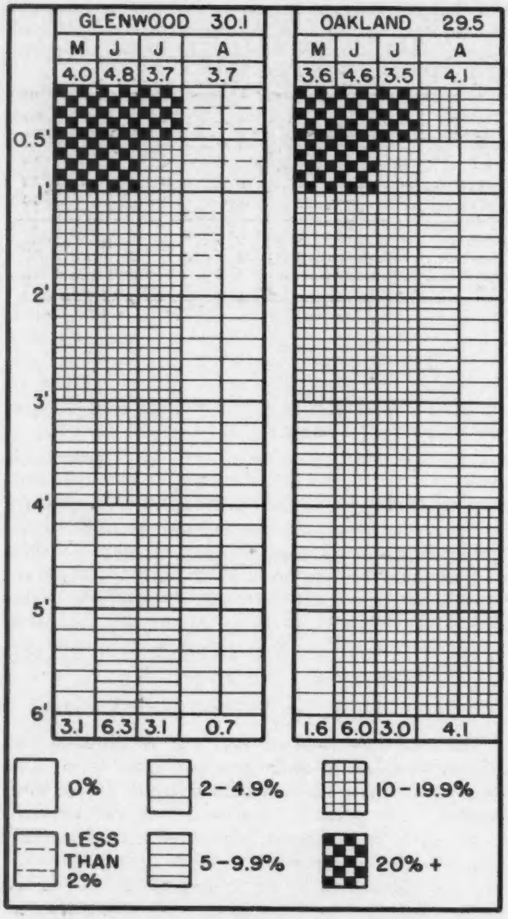

Fig. 62. Available soil moisture and precipitation at two Iowa stations during 1941.

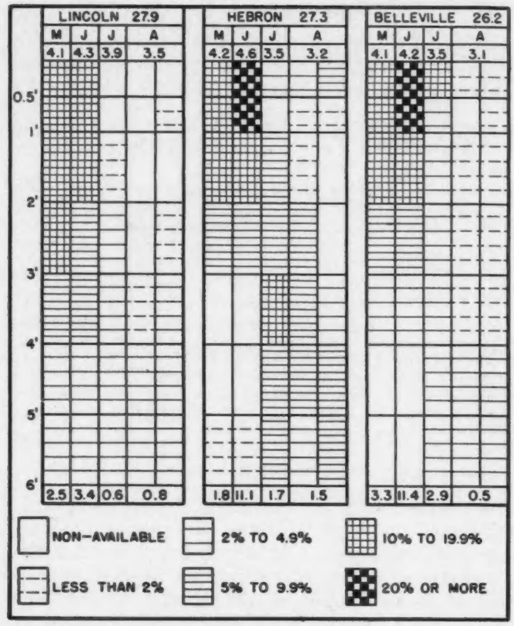

Fig. 64. Available water content of soil, mean annual and mean monthly precipitation, and current monthly precipitation at the Nebraska-Kansas bluestem stations in 1941.

Production of foliage was not much retarded at Hebron or Belleville, although the tops of the grasses had dried (Fig. 65). Foliage of little and big bluestem attained heights of 12 and 16 inches, respectively, which was 4 and 8 inches less than in Iowa.

At the western wheat grass stations, total summer precipitation was usually somewhat lower than at the preceding group, except Lincoln which had the lowest rainfall. Soil moisture was also considerably

Fig. 63. Representative dense growth of grasses and forbs at the Iowa stations in 1941. The grasses averaged 20 inches in height on September 1.

Fig. 65. Representative growth of bluestems and side-oats grama at Hebron, Neb. Height of bluestems was about 15 inches on August 27, 1941.

lower, as may be seen by even a casual comparison of Figures 64 and 66. This resulted in part from poorer infiltration of water and from the early absorption of soil moisture by a large crop of western wheat grass. Since this grass matures early, deficiency of subsoil moisture and even late summer drought had little effect in decreasing yields. Even by the first of May the foliage was 10 inches high and in the fourth-leaf stage. By the end of June the foliage level averaged 18 inches and the spikes, which were 3.5 to 5 inches long, were held on slender stalks 12 to 18 inches above the leaves. A view of the wheat grass prairie was as monotonous as that of a

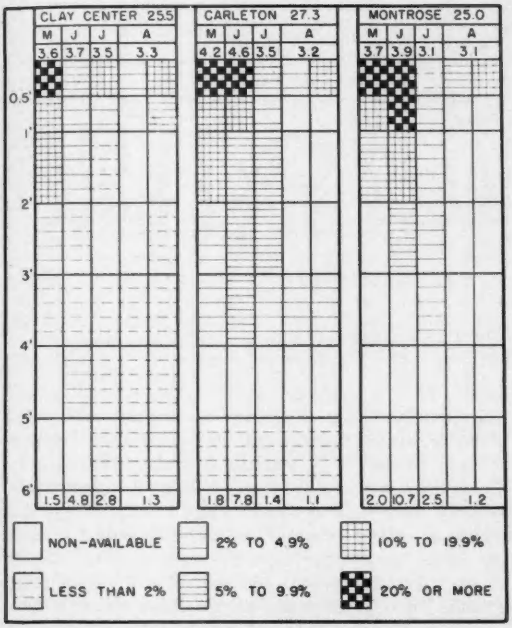

FIG. 66. Available soil moisture and precipitation at the Nebraska-Kansas wheat grass stations in 1941.

field of wheat. Above the foliage level each stalk bore only 1 short leaf. Submerged within this sea of grass (30 to 36 inches tall) were the few relic grasses and dwarfed forbs. *Amorpha canescens,* which averaged 24 inches in height in Iowa and 17 inches at the other bluestem stations, was here only 8 inches tall. Yield of hay was large (Fig. 67).

At the short-grass stations the previous years of drought had so depleted the native grasses and forbs that there were few to benefit by the excellent water supply in 1941 (Figs. 68 and 69). Moreover, at Phillipsburg and Hays, as generally throughout the area, a very early dense cover of *Hordeum pusillum* resulted from seed which had germinated the preceding fall. This weed grew to heights of 12 to 20 inches and quickly overtopped all of the remaining native vegetation. By shading it, development was greatly retarded, as was shown by the long, slender, light-green tillers of blue grama and stolons of

FIG. 67. View in the Carleton prairie on August 26 showing the large amount of hay produced in 1941.

buffalo grass. Even the pistillate flowers of buffalo grass were borne on long, slender flower stalks. There were numerous other weeds, as in 1940, which grew vigorously except where they were held in check by little barley. Among the most important were *Panicum capillare, Salsola pestifer, Amaranthus graecizans, Lepidium densiflorum, Lappula occidentalis, Monolepis nuttalliana,* and *Plantago purshii.* Where weeds were less abundant, as at Dighton, the short grasses were tillering profusely or spreading rapidly by stolons, but very few seedlings were found here or elsewhere (cf. Weaver and Mueller 1942). The best growth and recovery of the grasses occurred where weeds were absent, as at Dighton where patches of soil were completely revegetated by autumn. A few native forbs renewed growth at the other stations, but no forbs were found in the plots at Dighton. Mid-grasses, not found at Dighton, if alive had commonly only a few green tillers protruding from the periphery of the dry bunches.

By midsummer the matured little barley had, at a distance, the color and appearance of a ripened field of grain. Although dead, its shade still retarded growth of the short grasses. The most abundant

FIG. 68. One of the five 4-square-meter areas from which yields were obtained at Dighton, Kan. The short vegetation, consisting mostly of peppergrass, has just been clipped, showing much bare soil. June 25, 1940.

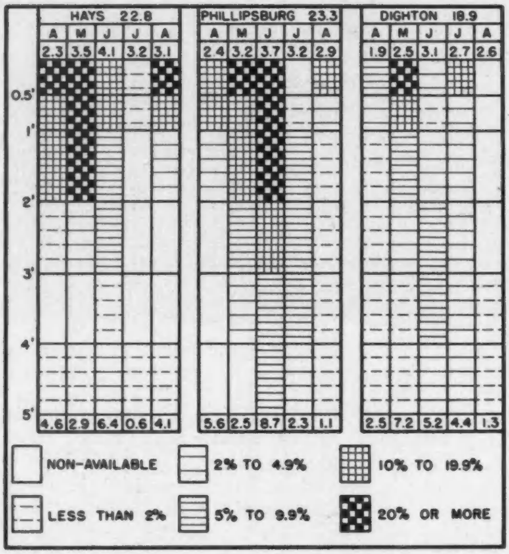

FIG. 69. Available soil moisture and precipitation at the Kansas short-grass stations in 1941.

forb was the very drought-resistant *Malvastrum coccineum;* a few other formerly common species, as *Astragalus mollissimus,* were observed for the first time in several years.

There was a short midsummer drought at Hays and Phillipsburg (and a little later at Dighton) when the short grasses became dormant, and cactus seedlings dried. But this was of relatively short duration and vegetation grew late into the autumn.

YIELDS IN 1941

Although only total yields are recorded from the western Kansas stations in order to conform with those from the other stations, they are from clippings made at various intervals. Only three were made at Dighton where weeds were few, but an additional earlier one on May 30 at the other stations was necessary to obtain the dead little barley and certain other weeds which might otherwise have been lost. Drought ended the growing season by September 13 at Dighton but the final harvest was made on October 18 at Hays (Table 19).

Yields of grasses and forbs at the Iowa stations were high and quite uniform. The average yield of the forbs was 15.7 percent of that of the grasses. The total average yield of hay was 10,912 grams per area sampled or 2.43 tons per acre.

Despite the midsummer drought at Lincoln, yields of grasses and forbs were only 16 percent less than at the other two bluestem stations in the Lincoln group. Average yield of forbs was 11.3 percent of that of the grasses. Total average yield of forage was 8,283 grams per area sampled or 1.85 tons per acre.

Yield of wheat grass was highest at Montrose and about 31 percent less at Clay Center, where it was

TABLE 19. Annual yield in grams of grasses and forbs at the several stations in 1941 and average annual yield per station group.

1941	Oakland	Glenwood	Lincoln	Hebron	Belleville
Grasses	9,902	8,956	6,609	8,030	7,685
Forbs	1,264	1,701	732	698	1,096
Total	11,166	10,657	7,341	8,728	8,781
Average	10,912		8,283		

1941	Clay Center	Carleton	Montrose
Wheat grass	8,547	9,752	12,422
Other grasses	142	1,091	45
Forbs	471	32	......
Weeds	1,528	......	......
Total	10,688	10,875	12,467
Average		11,343	

1941	Hays	Phillipsburg	Dighton
Short grasses	2,086	2,113	4,171
Mid-grasses	.....	329	.....
Forbs	159	571	.....
Weeds	4,677	7,572	243
Total	6,922	10,585	4,414
Average		7,307	

least. This is in direct accord with the amount of precipitation from February to June, which was about 18 and 11.5 inches at the two stations, respectively. Soil at both stations was dry to 6 feet in depth the preceding autumn. Yields of other grasses (mostly side-oats grama) were small, except at Carleton. Weeds were of considerable importance in the more open wheat grass stand at Clay Center where they composed 14 percent of the forage (Table 19). Total yields at the three stations were not so variable as those of wheat grass alone, since the weeds, forbs, and other grasses at Clay Center increased the total yield of hay to 98 percent of that at Carleton.

The average total yield of grasses, 10,666 grams, was 13 percent greater than that of the bluestems in Iowa and 43 percent greater than that of the grasses at the other bluestem stations. Quality, however, was greatly inferior. Native forbs constituted only 1.5 percent of the total yield. Average total yield was 11,343 grams per area sampled or 2.53 tons per acre.

At the mixed prairie stations yields of short grass slightly exceeded 2,000 grams at two stations but were nearly twice as great at Dighton. Mid-grasses occurred only at Phillipsburg, but in a small amount, being outranked by native forbs. Unlike the preceding year, relatively few weeds grew at Dighton but their yield at the other stations was two to nearly four times as great as the grasses. It is of interest that the station with the lowest total yield had the best cover of grass.

Average total yields of grasses in grams at the several station groups were 9,429 in Iowa, 7,441 at the second bluestem group, 10,666 at the wheat grass prairies where stems of wheat grass added greatly to weight of forage, but only 2,900 grams at the mixed prairie stations.

Relative yields of grasses, native forbs and weeds, and average total yields of 1940 are shown together with similar yields in 1941 in Figure 70. The yields

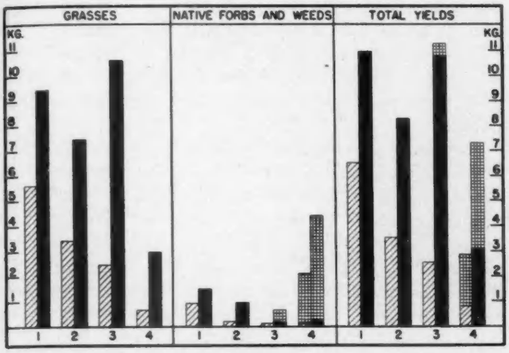

FIG. 70. Average yields of grasses, native forbs and weeds, and total yields of forage in 1940 and 1941 at the Iowa stations (columns 1), Lincoln stations (2), western wheat grass stations (3), and mixed prairie stations (4). Left hatch is for 1940; black for 1941; crosshatch indicates weeds.

of grasses increased at all stations during 1941. Increase in Iowa over the preceding year (columns 1) was 68 percent and at the Nebraska-Kansas bluestem stations 119 percent. Yield of western wheat grass was more than four times as great in 1941, as was also the yield of short grasses. In tons per acre, yields in 1941 were 2.10, 1.66, 2.38, and 0.65, respectively, from Iowa westward.

Yields of forbs increased but in a smaller degree; a large crop of weeds was produced in the short grass (columns 4) in 1940 but this was doubled in 1941.

Total yields were highest at the Nebraska wheat grass stations where weeds are included with the coarse-stemmed wheat grass. But when the economic criteria of quality of forage and actual utilization are applied, the value of the crop was greatest in Iowa each year and decreased regularly westward to the short-grass disclimax.

ATMOSPHERIC DROUGHT

Evaporation has long been used as an index in which the factors of insolation, humidity, temperature, and wind movement are more or less integrated. Data on relative evaporation losses as measured by the Weather Bureau at Lincoln and Hays are given for 1940 and 1941 in Table 20.

The data in Table 20 reveal two important facts: (1) that evaporation stress was higher each month at Lincoln in 1941 than during 1940; and (2) that, except in October, 1941, evaporation at Hays was always much higher than at Lincoln.

TABLE 20. Evaporation losses in inches from a free water surface as measured by the Weather Bureau at Lincoln, Nebraska, and Hays, Kansas.

Year	Station	Apr.	May	June	July	Aug.	Sept.	Oct.	Total
1940...	Lincoln ..	3.57	5.11	7.04	8.87	4.77	4.38	3.09	36.83
1940...	Hays....	8.45	11.25	13.87	16.88	10.32	9.23	7.45	77.45
1941...	Lincoln ..	4.44	6.21	8.41	11.42	6.15	5.82	4.58	47.04
1941...	Hays....	6.31	9.01	10.07	13.16	12.24	11.02	4.45	66.26

Atmospheric drought usually accompanies soil drought but it has probably been only a secondary cause of retarded growth. Even during the years of 1934, 1936, and 1939, when losses were greatest, it seems clear that high temperatures in grasslands were not the direct cause of death of plants, but one of the several factors which intensified drought. Evidence from both field and control experiments fully support this view (Weaver and Albertson 1940; Weaver and Mueller 1942). High evaporation rates nearly always accompany high temperatures in this midcontinental grassland. But only when the water supply of the soil has been depleted to low levels does high water loss through transpiration have much retarding effect upon growth of native plants in the field. They are adjusted to wide ranges of insolation, temperature, humidity, and wind. In general, these are all of greater magnitude, except for an inverse relation in relative humidity, progressively from Iowa to western Kansas.

To attempt to correlate plant production closely with any one or any combination of these factors would not be advisable under post-drought conditions of a plant cover, which is in itself extremely variable. The correlation between plant production at any group of stations during the dry year (1940) and the wetter one (1941) yields definite values. Likewise, a comparison of yields from areas of higher rainfall with those of lower precipitation, when studied in the light of change of types of vegetation and relative depletion of cover, is of great value in a quantitative interpretation of drought.

SUMMARY

A resurvey of vegetation both above and below ground was made in midwestern grasslands at the end of the great drought. It included the western portion of the true prairie in Iowa, eastern Nebraska and Kansas, and the mixed prairie, with its short-grass disclimax, in western Kansas and Colorado. Five prairies in western Iowa, 12 in true prairie west of the Missouri River, and 12 in mixed prairie in Kansas have been studied year by year since the inception of drought in 1933-1934. This is the record of their condition in 1940 near the end of the drought.

There was little damage to native vegetation east of the Missouri River. Elsewhere in true prairie *Andropogon scoparius*, which was formerly the most abundant upland grass, suffered the greatest loss. It entirely disappeared from many prairies, and was

reduced from about 55 percent basal cover to 5 percent elsewhere. *A. furcatus,* after heavy initial losses, has persisted or spread widely. Its percentage relation to the total remaining but often sparse cover is about the same as formerly. *Sorghastrum nutans* has all but disappeared from uplands and there is now less on lowlands than before the dry years.

Poa pratensis, formerly widely and uniformly scattered throughout, almost all died in pastures and drought-stricken prairies. Although absent from most prairies, in others it is plentiful in ravines and on less xeric slopes.

Stipa spartea withstood the drought well, and a continuous spread of this grass has taken place into bared or semibared areas regardless of slope, and even onto low ground. *Sporobolus heterolepis,* like needle grass, did not occur in some prairies. Although early losses from drought were high, such great increase has occurred that it is now often ten times more abundant than formerly.

Bouteloua curtipendula is so drought-resistant that it often persisted where all other mid-grasses succumbed. Formerly constituting only 1 percent of the prairie cover, it has increased so greatly almost everywhere that it now ranks as the second most important prairie grass.

Agropyron smithii has made a phenomenal increase from a species of very minor importance to one of first rank. This early growing, sod-forming grass alone has complete control over thousands of acres of grassland. During drought, nearly all other grasses failed to grow successfully in association with western wheat grass.

Bouteloua gracilis, formerly of very limited and local occurrence in true prairie, was harmed by desiccation the least of all species. It has spread so widely that patches can be found anywhere except where the original cover of mid-grasses persisted. *Buchloe dactyloides* formerly occurred even less frequently than the preceding short grass, but it has made good gains in those prairies where it was found. Both grasses have commonly intermixed with western wheat grass.

Grasses of less importance that have lost heavily include *Koeleria cristata, Panicum scribnerianum,* and *P. wilcoxianum. Sporobolus asper* and *Muhlenbergia cuspidata* have increased in abundance.

From a study of large numbers of quadrats before, during, and near the end of the drought, the percentage of basal cover of each species was calculated and these data were used as a quantitative basis for comparing gains or losses.

The seven most important grasses in true prairie in 1940 in order of their abundance were *Agropyron smithii, Bouteloua curtipendula, Andropogon furcatus, Stipa spartea, Bouteloua gracilis, Sporobolus heterolepis,* and *Andropogon scoparius.*

Three types of grassland occur in mixed prairie. The short-grass disclimax type is widely distributed over level or moderately rolling uplands. The little bluestem type is found on hillsides with rock outcrops and in shallow ravines. The postclimax, big bluestem type covers the lower slopes and deep ravines.

Andropogon scoparius has entirely disappeared from the short grass, and has been reduced in its own type from about 45 to 1 per cent. *A. furcatus* was reduced to about one fourth its former amount in the little bluestem type. In its own type, about four fifths of it was replaced by more xeric grasses.

Bouteloua curtipendula almost disappeared from the short-grass type, it made steady gains in territory left bare by the death of little bluestem, and in ravines and on lowlands it frequently replaced big bluestem. Species of Aristida disappeared from the short-grass type and suffered a high rate of mortality elsewhere.

Bouteloua gracilis and *Buchloe dactyloides* formerly constituted four fifths of the entire vegetation of the short-grass type. Extreme drought and burial by dust killed most of the short grasses. In contrast to these losses, which ranged from 50 to 100 percent of the cover, gains were made by blue grama spreading on hillsides and into ravines where mid-grasses had succumbed. Most lowlands also became more or less covered with short grasses.

Buchloe dactyloides formerly shared the area more or less equally with blue grama. In many places it entirely disappeared and nearly everywhere it was heavily damaged. Despite rapid and repeated local recovery, this species lost much more heavily than the more stable blue grama. The present, much depleted short-grass cover consists almost entirely of these two species, but buffalo grass constitutes probably not more than one third of the mixture.

Studies of numerous permanent quadrats in 1932 and 1940 revealed the increase or decrease of each perennial grass in the three types of mixed prairie. *Bouteloua gracilis* and *Buchloe dactyloides* are the species of major importance in the short-grass type. In the other types they are *Bouteloua curtipendula, Agropyron smithii, Bouteloua gracilis, Buchloe dactyloides, Andropogon furcatus,* and *Sporobolus asper* var. *hookeri.*

A comprehensive record of the weakening and death of forbs shows that their decrease was not gradual but sporadic, corresponding with the severity of drought. Many shallowly rooted plants were nearly all killed the first year; more deeply rooted ones often persisted for several years; some very deeply rooted forbs lost most heavily near the end of the drought.

Average number of long-lived native forbs found before the drought in bluestem prairies in Iowa, in Nebraska and Kansas, and in wheat grass prairies in Nebraska and Kansas was 85, 50, and 38, respectively. At the end of the drought it was, in the same order, 82, 41, and 21.

Relative size of the same species decreased greatly with increasing drought westward. *Amorpha canescens* decreased in height from 19 inches to 7 and then to 5 inches, and *Rosa arkansana* from 30 to 18 and finally to 6 inches.

Decrease or increase in abundance of forbs was ascertained from lists made before, during, and at the end of the drought. In a list each species was placed in one of 5 classes according to its abundance and ecological importance. In the Nebraska-Kansas true prairie, only 1 species increased in abundance at all stations, 11 changed but little, and 19 decreased considerably. In western wheat grass, 13 species disappeared entirely.

Species and ratings of long-lived forbs found at the end of the drought were ascertained for the undisturbed bluestem prairies in Iowa, the drought-depleted ones in Nebraska and Kansas, and the Nebraska-Kansas wheat grass prairies. Fifty-nine species of the more mesic forbs were found at the Iowa prairies only. Thirty-six species of more xeric forbs occurred at the more westerly bluestem prairies as well. Another group of 34 xeric species was found in the wheat grass prairies.

Only 17 species of native perennial forbs were found at the 15 stations in mixed prairie. Only one or two were abundant in any prairie. Ten of the most drought-resistant occurred sparingly before 1939, but thereafter only four.

Number of stems of forbs in two circles, 50 feet in diameter, was ascertained at each station. Average number of stems at the Iowa stations was 27,875, at the Nebraska-Kansas bluestem stations 7,109, and at the wheat grass stations only 1,083. At 14 stations in western Kansas, the average number of stems per unit area was only 23.

Occurrence and abundance of the most important long-lived forbs of uplands in 1940 are shown schematically. Only 5 species maintained approximately their predrought abundance; 41 species decreased in abundance. All maintained their usual abundance in Iowa, and all but 5 decreased in eastern Kansas and Nebraska. Among species mostly of mixed prairie and short-grass disclimax, 28 are listed. Three persisted in normal numbers, 14 disappeared, and the rest lost heavily. Another group of 13 species increased greatly in abundance during drought somewhere in true prairie or mixed prairie.

Grasses and forbs in true prairie died from desiccation in 1934-1936 only after they had absorbed the available water in the surface 3 or 4 feet of soil. Rainfall during the dry years was inadequate to moisten the deeper portion of this dry layer. Roots of new vegetation were confined to that portion of the soil moistened by current precipitation, and they were separated by a dry layer from the moist subsoil.

Loss of the plant cover greatly hindered water infiltration as did also the covering of dust, and the invasion of *Agropyron smithii.* The period necessary for an inch of water to infiltrate into bare soil was 2.8 times as long as that for infiltration into the same kind of soil which supported a good cover of predrought prairie grasses.

Resurvey of root systems in true prairie involved an examination of (1) relic grasslands where the original plant population was little affected above ground, of (2) badly denuded areas where only widely scattered relic or invading grasses occurred, and of (3) half-bared places where relic grasses or invading species had increased.

Root habits were normal under the first condition. Under the second, much space between the plants was almost free from living roots. Depth of roots corresponded with that of current rainfall penetration, about 2 to 2.5 feet.

Roots of relic *Andropogon furcatus* were confined to the surface 2.5 feet and those of invading *Agropyron smithii* to about 2 feet. Below, a dry layer of soil with water unavailable for growth extended to about 5 feet. Certain forbs with roots only 5 to 6 feet deep had succumbed, but others which had penetrated to depths of 10 to 17 feet before the drought survived, although greatly dwarfed. They obtained water in part from a slightly moist subsoil that had not received additional moisture since 1934.

In mixed prairie, bisects in the upland short-grass type revealed that roots of *Bouteloua gracilis* and *Buchloe dactyloides* were fewer in number and shallower in depth of penetration. A former root depth of 4 to 5 feet at Hays, Kansas, had been replaced by one of about 18 inches. Under lighter precipitation westward, the depth was rarely more than 12 inches. Most old roots of forbs had died. The few that grew during the drought were much shallower.

In ravines where additional water was supplied by runoff so that the deep soil was moist, the roots grew deeper as drought increased. The roots of *Andropogon furcatus, Agropyron smithii,* and certain other grasses extended a foot deeper and branched more profusely in the deeper soil than in 1933. Those of *Aster multiflorus, Vernonia baldwini,* and other coarse forbs doubled their length.

Amount of available soil moisture and yield of grasses and forbs were ascertained at four groups of stations during the dry year 1940, and the moderately wet one 1941.

In 1940 at the western Iowa stations, rainfall was sufficient to keep the soil continuously moist to a depth of 6 feet, except for a moderate midsummer drought. Three bluestem prairies, undamaged by former drought, gave a high and uniform yield of grasses. Yield from one clipping in September was about the same as the sum of four clippings on sample areas of similar size made at monthly intervals. Early yields of forbs were high, but after a second clipping, they decreased greatly. Total yield of forage was 1.45 tons per acre.

In the drought-damaged bluestem prairies westward, severe drought began in midsummer and available soil moisture was exhausted to a depth of 5 or 6 feet. Yield was about the same whether obtained in one or four harvests. It was only 0.80 ton per acre or 55 percent of that in Iowa.

Where western wheat grass had replaced the bluestems, soil moisture was available only in spring and early summer. Yield in May was heavy but light or none thereafter. Yield of four clippings and of a

single harvest were nearly equal. Total yield was only 0.56 ton per acre or 39 percent of that in Iowa.

In western Kansas where drought and dust had reduced the basal cover of the short grasses to only 10 percent normal, drought began in May. Usually the surface foot alone had available water, but only temporarily and at widely separated intervals. Average yield, including weeds, was 0.61 ton per acre. Yield of grasses and native forbs alone was only 13 percent as great as that in Iowa.

In 1941 in Iowa, water content was high to a depth of 6 feet at least until August, and vegetation flourished. At the second group of stations, both rainfall and soil moisture were less, but the general pattern of water distribution was the same, with moderate drought in late summer. Heavy rainfall at the wheat grass stations resulted in an abundance of soil moisture, at least until the wheat grass had ripened. An excellent supply of soil moisture prevailed at the Kansas short-grass stations. It promoted a rank growth of *Hordeum pusillum* and other weeds which greatly retarded the development of the much depleted native grasses.

Average yield in Iowa was 2.43 tons per acre, of which the native forbs produced about 16 percent. The Nebraska-Kansas bluestem prairies yielded 1.85 tons per acre, about 11 percent being native forbs. Yield at the wheat grass stations was 2.53 tons per acre, of which 1.5 percent was supplied by the native forbs. This was 4.5 times as great as the yield of the preceding year, and slightly greater than that in Iowa. Yield of native grasses at the short-grass stations was only 0.65 ton per acre; that of grasses and weeds together was 1.63 tons.

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